ALPINE THERMAL DYNAMICS AND ASSOCIATED CONSTRAINTS ON THE BEHAVIOR OF MOUNTAIN GOATS IN SOUTHEAST ALASKA

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A

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Abstract

Alpine Caprinae, including mountain goats (*Oreamnos americanus*), have been described to be sensitive to temperature changes within their summer range and consequently may be forced to select habitats that allow for the maintenance of a stable core temperature on warm days. Survival may be inhibited if warm ambient temperatures cause mountain goats to reduce time foraging or if too much time is spent on thermoregulatory habitat selection. I investigated mountain goat behavioral activity budgets across alpine temperature gradients in Southeast Alaska using focal animal sampling and scan sampling techniques. I tested the effects of temperature on mountain goat activity and mountain goat elevation. Coupled with the behavioral investigations, I simultaneously monitored elevational temperature gradients using an array of passive thermistors. By monitoring hourly temperatures and deriving near-surface lapse rates, I demonstrate the utility of downscaled, region-specific temperature-elevation profiles for ecological applications rather than making inferences based on broad spatial models. Except in winter, lapse rates within the study area were between -0.3˚C $100m^{-1}$ and -0.4˚C $100m^{-1}$, and were not inclusive of the global mean environmental lapse rate (-0.65˚C $100m^{-1}$). Mountain goats within the study area demonstrated behavioral conservation of their activity budgets by altering their orientation through space and time, rather than incurring thermal and/or nutritional deficits. In addition, the animals took advantage of cooler temperatures at high elevations to bolster thermoneutrality. I highlight the need for behavioral ecology research that links physiological mechanisms and mammalian life history in an effort to predict the fate of a sentinel wildlife species as it copes with a changing environment. Indeed, such indicator species are invaluable to understanding the dynamics of change in ecosystem structure, function, and phenology. Given current warming trends and projections of changing climate regimes being more pronounced at higher latitudes, there is a marked need to better understand thermoregulatory constraints on faunal behavior and the effect of changing landscapes on the distributions and survival of wildlife populations in Alaska.

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Chapter 1 – Background

1.1 – Compendium of Scope of Global Change

The result of current integrative physical scientific research, spanning the myriad of disciplines therein, has illuminated the fact that the Earth is experiencing a ubiquitous and unprecedented period of global change. Of particular note are changes to three of the four physical spheres that comprise the planet, those being: the atmosphere, hydrosphere, and biosphere. Interest in measured changes to the three spheres is largely due to their respective proximity and interaction with all biotic and abiotic components, as well as the comparative ease at which they can be studied. We recognize, however, that the forcings responsible for driving this global change likely have little effect on the fourth sphere: the solid Earth (comprised of the crust, mantel, and core).

The atmosphere, comprised of the various gas constituents surrounding the planet, is a crucial effecter of both the physical and biotic systems on Earth. Critical atmospheric changes noted in recent decades include: shifts in the concentrations of certain gases, depletion of ozone (O_3) within the stratosphere, increased surface temperatures, changes in atmospheric circulation patterns, and the prevalence of extreme meteorological events. Of the gases that make up the atmosphere, greenhouse gases are those that that trap or reflect radiant energy from within the atmosphere, rather than allowing it to escape (Kump et al., 2010). Greenhouse gases of marked concern are carbon dioxide (CO_2), nitrous oxide (N_2O), methane (CH_4), and anthropogenically derived chlorofluorocarbon compounds (CFCs) (Kump et al., 2010; Pachauri et al., 2014). CFC compounds are widely implicated with the depletion of O_3, resulting in an increase in the amount of ultraviolet radiation (UV) capable of passing through the atmosphere. Increased UV radiation subsequently has pervasive deleterious effects on biota. CO_2, N_2O, and CH_4 are implicated with raising the surface temperature of the planet (among other effects discussed later). The Intergovernmental Panel on Climate Change (IPCC) noted that the average rise in surface temperature (land and ocean inclusive) since the late 1800s is 0.85°C (1.53°F) and that greenhouse gases currently exist in more prodigious concentrations than they have in the last 800,000 years (Pachauri et al., 2014). Current greenhouse gas concentrations are likely higher-still than those experienced over vastly larger temporal scales (>800,000 years). Those data, however, are dependent solely on the successful extraction of ice cores, limiting the scope of how far back in time global surface temperature can be estimated. By the end of the 21st century, an additional 2°C (3.6°F) increase in average global surface temperatures has been projected (Pachauri et al., 2014). Extrapolating from this temperature increase, an irrevocable consequence of increased global temperatures is a change in atmospheric circulation. Weather as we know it is driven by atmospheric circulation, which in turn, is driven by the gradient of heat energy within the atmosphere. The magnitude of heat energy received in equatorial regions is largely

disproportionate to the dearth of heat energy received near the poles, engendering a dissimilarity of atmospheric pressures and densities between the two regions (Kump et al., 2010). The amalgamation of the planet's rotation, the flow of energy from high to low (creating wind), and the inclusion of water vapor (into the system) from land and sea, produce all of the weather variation on Earth. In the coming years, increased heat energy inserted into the system will unequivocally shift the patterns of atmospheric circulation; in some cases, causing a higher magnitude of meteorological extremes (Pachauri et al., 2014). Indeed, the landmark papers by Emanuel (2005) and Webster et al. (2005) highlighted that increased surface temperatures have precipitated increases in both the frequency and destructive potential of hurricanes. Further, if atmospherically driven surface temperatures continue to warm, this trend can only perpetuate to a higher degree (Emanuel, 2005; Webster et al., 2005).

Of additional concern regarding global change are a suite of modifications to Earth's hydrosphere. Though the hydrosphere includes terrestrial freshwater hydrological systems (e.g., lakes, rivers, and estuarine basins), herein, for introductory descriptive purposes, I concentrate my global change foci on Earth's oceans and reservoirs of ice (otherwise known as the cryosphere). As 70% of the planet's surface is ocean-covered, measureable changes to the hydrosphere are of particular concern. As atmospheric change has triggered an increase in surface temperatures, much of that increase affects the Earth's oceans. The IPCC (Pachauri et al., 2014) notes that oceans have warmed on average 0.33°C (0.6°F) just in the last 30 years, and 90% of heat energy added to Earth system as a whole within that 30 years was stored by the oceans. Ocean temperatures are intimately linked to localized weather trends in all areas of the globe and, as such, warming oceans will contribute to future weather variability. The primary driver of ocean-regulated localized weather trends is surface (ocean) water circulation, which is governed by atmospheric wind currents and contributes nearly the same amount of heat energy transport from the low latitudes to the poles as the atmosphere does (Kump et al., 2010). The ocean is additionally coupled with the atmosphere, in that, it takes up large amounts of CO_2, acting as a global carbon sink. That said, only the surface water of oceans interact with the atmosphere to exchange CO_2 (a miniscule volume of water compared to that of the deep ocean), and the resulting chemical reactions responsible for this process precipitate excess hydrogen cations (H^+) (Kump et al., 2010). This process effectively lowers the pH of the oceans making them more acidic. Since the late 1800s, the acidification of the world's oceans has caused the pH to drop by 0.1 units (Pachauri et al., 2014). Staggeringly, this has resulted in a 26% increase of ocean acidity, undoubtedly contributed to by the rise of atmospheric CO_2 (Pachauri et al., 2014). Exacerbating the aforementioned changes to the hydrosphere is a well-documented (and ominously projected) rise in sea level. Within the last century alone, sea level has risen by an average of 19cm; to which there has been no analogous rate within the last two thousand years (Pachauri et al.,

2014). This rise in sea level is partly due to a second component of the changing hydrosphere: the melting of the cryosphere.

Though the exact global extent of glacial ice retreat and melting cannot be currently estimated due to a lack of measurement across the vast majority of Earth's ice-covered sites, the IPCC notes that in most areas of the world during the last 25 years, resident glaciers demonstrated a negative mass balance (i.e., have been losing volume) (Watson and Albritton, 2001). A vast majority of Earth's glacial ice reservoir is located on Greenland and Antarctica. Though the specific processes by which melting occurs in these respective areas varies, the partial melting of the Antarctic and Greenland ice sheets could translate to a sea level rise of several meters (m). Taken overall, the amount of water displaced to Earth's oceans from all the ice in Greenland and Antarctica would translate to a sea level rise of around 72m (Kump et al., 2010). For a moderate CO_2 emissions scenario, the IPCC (Bernstein et al., 2007) reports that the resultant melting of glacial ice could translate to a 20-50cm rise in sea level by 2100. Glacial extent under a low emissions scenario may decrease by 15-55%; whereas while the high emissions scenario projected decrease is 35-85% (Pachauri et al., 2014).

The last and arguably most alarming facets of global change to be considered are those within the biosphere. Herein, I take an ecosystems inclusive approach when regarding the biosphere to include all life on Earth and its associated respective habitats. The gravity of a loss in biodiversity (including genetic diversity) is underscored by the elimination of crucial ecosystem services that drive the livable stasis of the planet by its organisms. Examples of such ecosystem services include clean water and air, food, carbon cycling, soil nutrient regulation and reclamation, medicines, disease and pest control, recreation, and energy (Watson and Albritton, 2001). Though estimations of the loss of biodiversity are varied, and said appraisals are likely deficient due to a lack of comprehensive biotic description, the current period of global change undoubtedly includes an extraordinary rate of species loss worldwide. Moreover, recent research attempts to quantify biodiversity loss have noted that global biodiversity loss is currently accelerating (e.g., Vié et al., 2009) and the previously-noted conservative estimates of species loss indicate that the current period of global change (if species loss rates continue) will officially mark the sixth global mass extinction (characterized by a 75% or more loss of species under short geologic time scales) in as soon as two and one half centuries (Barnosky et al., 2011; Dirzo and Raven, 2003). The primary impetus for such species loss on Earth is anthropogenic habitat destruction. For terrestrial habitats and biota, this destruction is engendered largely by deforestation practices (Kump et al., 2010). Such losses of biodiversity through deforestation have reverberating and exacerbating effects on global change, as well. This coupling is both exemplified and epitomized by the deforestation of tropical forests (Foley et al., 2000). Of all the worlds floral and faunal species, one half (or more) exist in tropical rainforests, while these biomes only account for 7% of the land area on the planet (Kump et al. 2010).

Eradication of these habitats though, fosters not only biodiversity loss, but an inhibitor of mitigating potential for an increase in atmospheric CO_2. Carbon fixation by Earths flora takes place as carbon dioxide is taken up for use in photosynthesis and sequestered in the tissues of plants. The terrestrial environment as a whole is responsible for between 1.6 and 4.8 Pg ($1.6\text{-}4.8 \times 10^{15}$g) of carbon annually with the neotropics contributing 1 to 6 tons of carbon uptake per hectare per year alone (Ometto et al., 2005). Deforested terrestrial regions are, in turn, ineffective when compared to their primary forest counterparts at recycling carbon from the atmosphere; a role that has been estimated to potentially offset 22% of annual anthropogenic carbon dioxide emissions (Foley et al. 2003).

Global change to the biosphere has been widely established in the observation of shifts in the distributions of both species and whole biomes as a result of increasing surface temperatures (DellaSala et al., 2011; Loarie et el., 2009; Mawdsley et al., 2009; Pachauri et al., 2014; Pereira et al., 2010; Wang et al., 2012a). The sweeping trend of this shift is a pole-ward migration of biota. Increasing habitat fragmentation may pose a formidable hindrance on the ability of biota to adapt to shifting surface temperatures by engaging in successful northward migration (i.e., decreased mobility potential). The amalgamation of varied organismal resilience, mobility potentials, and the spatial distribution of evolving surface temperatures will likely produce a suite of unique and yet-to-be observed ecosystems across the planet (DellaSala et al., 2011; Loarie et al., 2009). A species or system's ability to match or tolerate the pace of rising surface temperatures will inevitably govern whether or not they persist, as the planet's geospatial, latitudinal mean velocity of temperature increase has been calculated to be 0.5 – 1.5 km year^{-1} (Loarie et al., 2009; Pereira et al., 2010). The northward migration of floral species is supported by the paleo-fossil record during historical periods of temperature increase (DellaSala et al., 2011; Pereira et al., 2010). Earth's northern temperate rainforests and northern boreal forests, for example, are expected to die back at their southern termini while their northern range limits will migrate pole-ward, spatially extirpating/colonizing the arctic tundra and boreal forest respectively (DellaSala et al., 2011; Foley et al., 2000; Pereira et al., 2010). Likewise, mixed temperate deciduous forests are expected to migrate northward, encroaching on regions of temperate coniferous rainforest dieback (DellaSala et al., 2011).

1.2 – Climate and the Temperature Proxy

The combination of forcings within the atmosphere, hydrosphere, and biosphere cause changes to: global surface temperatures, weather anomalies, sea level rise, marine acidification, carbon cycling, and species distributions. Taken together, I distinguish the conglomerate of the global energy balance/flux, atmospheric activity and chemistry, localized surface-level thermal and moisture regimes, and its effects and interactions with the biosphere, hydrosphere, and cryosphere as coalescing to generate a region's climate. Specifically defined, climate hereafter will be considered to encompass both the state

of, and variation of weather conditions for a designated region, averaged across a specified temporal scale. Subsequently, the average climate of a region taken across a 30-year temporal scale is referred to as a climate normal. Statistically speaking, climate variability is regarded as the standard deviation calculated for the state of a region's climate across a specified temporal scale (Roe and O'neal, 2009). Climate, thus, epitomizes the nature of global change because of its interactions and intrinsic dependency on the state of the atmosphere, hydrosphere, and biosphere.

Global climate variation is governed by temperature gradients in both land and sea surface temperature. At the most fundamental level, the substantially larger amount of thermal radiation received at Earth's equatorial regions (compared to polar regions) causes energy to flow from high concentration to low, creating the wind and the weather systems experienced in terrestrial regions. Likewise, the circulation and transport of warm sea surface water to the poles via wind creates the large gyres and currents also responsible for weather experienced in different geographic locations. Within the atmosphere, increased temperatures influencing Earth's oceans precipitate stronger and more frequent cyclones (Emanuel, 2005; Webster et al., 2005). Meteorologically, the diurnal variation in weather measured in mountainous regions is defined by channeled air flow, drainage, or pooling (where possible) owed to localized thermal disparities (Gustavsson et al., 1998). Within the hydrosphere the integration of: a buildup of warm water surrounding Southeast Asia and Oceania, the thermal expansion of the warmed (sea) surface layer, and the ocean-wide temperature difference between the aforementioned region and the cold, Antarctic-fed waters off the west coast of South America, culminate in an enormous thermal wave (otherwise known as the El Niño Southern and Pacific Decadal Oscillations) radiating across the Pacific; significantly affecting the weather and climate of whole continents (e.g., Bonfils et al., 2008) across year-long scales (Kump et al., 2010). Within the cryosphere, both rates of ice flow and glacial extent are dependent on temperature (Roe and O'neal, 2009).

Nearly innumerable effects of thermal regimes on organisms and ecosystems can be illustrated within the biosphere; ergo, the following contains only a brief enumeration of temperature associated biotic canons. Within the biosphere, tolerances for temperature govern: growing season, geographic biotic ranges (e.g., DellaSala et al., 2011; Rieman et al., 2007), floral maturation and growth rates (e.g., Bolstad et al., 1998; Bonfils et al., 2008), and the myriad of respective organismal morphological and life history characteristics. Temperature unequivocally affects rates of plant phenology, carbon cycling, and respiration, thus, also affecting water requirements and photosynthetic capability (Bolstad et al., 1998). The temperature-soil moisture gradient, in fact, represents a primary regulator of the geographic distribution of plant species (Lookingbill and Urban, 2003). Bolstad et al. (1998) further note, that for trees, the synergism of temperature with soil, terrain complexity, and insolation affect not only growth but forest species composition, the generation of detritus, and the responsiveness to disturbance. For wildlife,

temperature and associated regional climates have historically acted as the primary fundamental catalysts of adaptation and evolution (Mawdsley et al., 2009). Further, air temperature not only regulates community structure, but also the energetic cost of metabolism within an environment (Kearney and Porter, 2009; Natori and Porter, 2007; Porter et al., 2000). Among terrestrial endotherms, air temperature regulates body size optima, in that larger body sizes require lower temperatures to maximize the discretionary mass/energy needed for growth and reproduction (Porter et al., 2000). This axiom is evidenced by Bergmann's rule, whereby animals tend to be comparatively larger in colder climes (Porter et al., 2000). In both endotherms and ectotherms, certain behaviors are critically and directly manifested by environmental temperatures; resulting in thermoregulatory habitat selection in an effort to minimize heat stress (e.g., Aublet et al., 2009; Long et al., 2013; Natori and Porter, 2007; Sinervo et al., 2010).

The various considerations, predictions, and projections of the effects of warming global surface temperatures on organisms are primarily derived from knowledge of the thermal tolerances and preferences of organisms, and their respective ranges of productivity. Moreover, the spatial velocity of climate change itself, measured to predict the necessary speed at which biomes and their organisms must acquiesce, is calculated in terms of warming surface temperature shift (Loarie et al., 2009; Pereira et al. 2010). Thus, we consider that hereafter, surface temperature is paramount as an effective and appropriate proxy for measuring or inferring climate, climatic change, and climatic variability, especially with regard to ecological or zoological investigations.

1.3 – Climatic Trends in High Latitudes and/or Complex Terrains

Recent global climate change (in terms of surface-temperature warming) has been the most pronounced at high latitudes (Forland et al., 2002; Mountain Research Initiative, 2015; Serreze and Barry, 2011). Moreover, future projections of climate scenarios note that in high latitude regions, increases in humidity, precipitation, and surface temperatures are driven by, and susceptible to the atmospheric effects of increased concentrations of greenhouse gases (Forland et al., 2002; Forland and Hanssen-Bauer, 2003; Mountain Research Initiative, 2015). The spatial/geometric mean velocity of increased surface warming has, as well, been projected to be higher at high latitudes (Loarie et al., 2009). Terrestrial high latitude climatic shift is synergistically exacerbated by the perpetuation of two earth system feedbacks: the ice-albedo feedback and the forest-tundra albedo feedback (Foley et al., 2000; Forland and Hanssen-Bauer, 2003; Giorgi et al., 1997; Mountain Research Initiative, 2015; Serreze and Barry, 2011). The first progresses as increased air temperatures decrease the distribution and spatial extent of persistent snow and ice, increasing the extent of darker, heat-absorbing surfaces, which in turn promote further surface warming. The second proceeds as surface temperatures facilitate permafrost thaw, promoting the colonization of tundra regions by trees, which likewise due to their darker hue (than tundra surfaces)

promotes further surface warming. Though I abridge my high latitude discussion to focus on terrestrial systems, a third major feedback involved in high latitude warming requires mention, in that, the ice-albedo feedback additionally includes a marine component, whereby, annual sea ice extent (or the lack thereof) contributes to surface warming near the poles because of the lower reflectivity and higher thermal absorption of the ocean compared to a snow/ice-covered surface. An exemplar of the extent to which the process of high latitude climate shift has progressed was noted by Forland et al. (2002), in which they describe a 0.6° C per decade increase in air temperature in the Svalbard Archipelago, north of mainland Europe in the Arctic Ocean, having been observed since the mid-1970s.

Chapter 2 – Research Conspectus

2.1 – Near-Surface Lapse Rates in Southeast Alaska

As climate variability is estimated to be amplified by complex terrain, and climate warming effects on hydrologic and biophysical systems is predicted to be more pronounced at higher latitudes, the need for downscaled climate research in Alaska remains at the forefront of scientific study. Recent research has shown that within Alaska, as many as 13 individual climate zones can be demarcated. This further highlights the need for downscaled regional study of the climatic trends unique to Southeast Alaska (Bieniek et al., 2012). Unique physiographic characteristics of Alaska's Southeast Panhandle including proximity to the Pacific Ocean, a dominantly mountainous landscape, a high density of glaciers and icefields, and the presence of extraordinarily undisturbed expanses of coastal temperate rainforest, must admix to produce a suite of region-specific lapse rates found nowhere else on Earth. The incremental decrease of air temperature with increasing elevation (near-surface lapse rates) in this region is also likely unique and may demarcate ecotone boundaries, affect ecosystem phenology, or the biology of wildlife inhabiting this region. As such, this study aims to address the following objectives: 1) to accurately and precisely characterize daily and monthly mean near-surface lapse rates for my study area across spatiotemporal scales, 2) to assess the reliability of a mean environmental lapse rate in regard to its use for climate modeling and projection within the Southeast Alaska region, and 3) to assess the utility of lapse rates calculated during this study for temperature-elevation inference in biological studies. To my knowledge, this is the first attempt to characterize near-surface lapse rates for Southeast Alaska.

2.2 – Mountain Goat Behavioral Ecology

Compelling evidence that alpine ungulates may be used as ecosystem indicator species not only supports the exploration of ecological research on mountain goats in general, but also underscores a unique opportunity for Southeast Alaska as mountain goats are the only alpine ungulate present within this geographic region. This study aims to address the following objectives: (1) to evaluate the effects of climate warming on the proportion of foraging behavior exhibited by mountain goats in their summer habitat, (2) to identify the primary behavioral mechanisms by which mountain goats thermoregulate, (3) to identify any existing trade-offs between optimum forage and thermoregulation, and (4) to investigate potential linkages between montane thermal gradients (i.e., lapse rates) and animal behavior. I offer the overarching hypothesis that if mountain goats are sensitive to thermal stress, then they will engage in behaviors that reduce exposure to heat. The first prediction regarding this hypothesis is that the proportion of time mountain goats spend foraging is lower on hot days than on cool days. Secondly, I predict that mountain goats will use high elevation sites on warm days because inherent lapse rates cause air

temperatures to be cooler than proximal lower elevation sites. To my knowledge this is the first attempt at investigating behavioral thermoregulatory behavior in conjunction with a downscaled lapse rate study for any species.

Chapter 3 – Introduction

3.1 – Montane Climate and Near-Surface Lapse Rates

3.1.1 – Associations of Climate with Complex Terrain

Studies of warming surface temperatures and increased climate variability in the terrestrial systems have revealed a stronger pattern of change at higher elevations compared to low elevation sites (Beniston et al., 1997; Giorgi et al., 1997; Mountain Research Initiative, 2015). This finding is an important consideration in the study of climate impacts on terrestrial systems as increased precipitation, earlier snow melt, and volume of runoff have marked ecosystem-level effects, especially on localized hydrological regimes (Giorgi et al., 1997). The combined results of high elevation studies investigating climate changes within the last century have revealed a strikingly larger amplitude (e.g., see Figure 1 in Beniston et al., 1997) of temperature transmutation than those found at broader global and hemispheric scales (Dedieu et al., 2014). These patterns suggest that montane/alpine systems can be used as an early detection mechanism and/or metric for other various Earth systems (Giorgi et al., 1997).

The climate of montane regions is especially complex, the respective nature of which is owed to four determinants that are inherent to localized systems: topography, latitude, elevational extent, and the continent in which a given mountain system exists (Barry, 1992; Mountain Research Initiative, 2015). Topographic variation affects temperature and precipitation regimes due the amount of solar radiation received by a given mountain slope (Barry, 1992; Lundquist and Cayan, 2007; Rolland, 2003; Tang and Fang, 2006). The elevational extent of mountains denote differences in the temperatures, densities, and pressures of air that govern localized wind speeds, volumes of precipitation received, and amount of evaporative water loss present (Barry, 1992). The latitude of a mountainous region governs day length and the seasonal variation of solar input, manifesting in localized differences in snow accumulation and temperature range (Barry, 1992). Finally, continental assignment characterizes weather trends/variability and temperature range, resulting in snow line altitude differences (Barry, 1992). The composite set of topographic (i.e., aspect, slope, and elevation) variables with the aforementioned mountain climate determinants creates a highly unique and complex meteorological regime. In spring for example, a synoptic weather system could interact with mountains to bring rain to low lying sites (promoting snow melt) and induce snow accumulation in the alpine; whereas in winter, the absence of cyclonic systems may promote snow persistence in the lowlands, while inversions promote snowmelt in the alpine (Barry, 1992).

A novel characteristic of mountainous regions is the presence of distinct climatic and ecotonal zones formed by the vertical distributions of temperature and precipitation regimes (Beniston et al., 1997;

Becker et al., 2007; Peterson et al., 1997). These zones occur over short distances and exhibit stark contrasts in susceptibility to warming temperatures (Becker et al., 2007). This fine-scale variability in climate and ecotone conditions drives relatively high biodiversity across relatively small spatial scales in montane systems (Becker et al., 2007; Diaz and Bradley, 1997). Montane zones of ecotone and climate also effectively mirror the vegetative distribution, ecosystem structure, and thermal characteristics observed in the large-scale global latitudinal bands of non-mountainous regions (Beniston et al., 1997; Peterson et al., 1997). As such, the study of mountain climate and climatic variability is of critical importance for the ubiquitous effort to understand an ecological future resulting from past and current environmental changes.

The ecological and zoological value of climate research in high-latitude, high-elevation regions thus appears to lie with temperature gradients inherent to all mountainous regions. As high elevation sites are cooler than proximal low elevation sites (e.g., Kattel et al., 2013) mountainous regions may serve as a type of buffer to surface temperature warming because high elevation sites may harbor temperatures within the scale of thermal tolerance for many organisms (Loarie et al., 2009). Given that climate change may be more pronounced at higher latitudes, when considering its impacts on terrestrial systems worldwide, this buffering effect, slowing the manifestation of surface warming (compared to low elevation systems), may result in mountainous regions acting as refugia for a variety of species in the future (Loarie et al., 2009). The ecosystem services-related value of mountainous regions is of global importance as they supply half of Earth's human population with various services, and are inhabited by 10% of Earth's human population (Beniston et al., 1997; Dedieu et al., 2014). The reliance of human life and proliferation on mountainous regions, from the standpoint of both economics and even basic fundamental needs (e.g., water and food), engenders great concern over climate impacts on these systems. All else being equal, fluctuations and deviations of precipitation in these areas have been recorded and are subsequently projected to intensify (e.g., Giorgi et al., 1997). As such, detrimental impacts to the freshwater regimes on which agriculture, industry, and general domestic needs are reliant, are of great concern and affect all the previously mentioned human needs, even in regions which are proximally distant from mountains themselves (Beniston et al., 1997; Dedieu et al., 2014).

3.1.2 – Regional Downscaling and High-Density Instrumentation

A current challenge when attempting to monitor, evaluate, and model climatic trends in complex terrain is a lack of regional downscaling; that is, assessing climate of a region at fine temporal and spatial resolutions (Beniston et al., 1997; Holden et al., 2011; Thorton et al., 1997; Wang et al., 2006; Wang et al., 2011). This issue mainly stems from the inherent logistical and economic challenges of deploying meteorological monitoring equipment in mountainous regions. As such, recent studies pertaining to

mountain climates and climate change highlight that accuracy and precision are often hindered, limiting the explanatory power of climate models (or trends) because they are based on sparse station records (Chronopoulos et al., 2008; Dodson and Marks, 1997; Tank et al., 2002; Stahl et al., 2006; Wang et al., 2006). Especially when sparse station records are obtained from low elevation sites, consistent errors are often made due to a lack of consideration for topographic complexity and resultant temperature measurements are regularly overestimated (Bolstad et al., 1998; Lookingbill and Urban, 2003).

As a result of the topographic and physiographic complexity of mountainous terrain, surface temperatures are widely described to vary across spatial scales (Barry, 1992; Holden et al., 2011; Stahl et al., 2006). This presents challenges in evaluating regional climates, as the most readily available climate datasets and interpolation tools are based on gridded models that either fail to account for topographic complexity, or over-generalize climate for broad geographic regions. In terms of ecological studies, the amalgamation of sparse meteorological station deployment and course resolution gridded datasets results in the inability to infer relevant variables in complex terrain such as: surface temperature, snowmelt rates, growing degree days, soil moisture, plant phenology, or synoptic weather conditions (Garen and Marks, 2005; Holden et al., 2011, Stahl et al., 2006; Wang et al., 2012a). Indeed, the majority of global circulation models (GCM) used to predict/project future regional temperatures produce a gridded output at a resolution of 100 – 200km (Daly, 2006; Wang et al., 2011). That said, a distinction is made between interpolation of climate data for GCM predictions and the spatial interpolation from weather stations used to produce mapped thermal surfaces (e.g., Wang et al., 2012), though the spatial and temporal sampling resolution of both efforts should be advanced. For example, models may be created for a large spatial region and claim high resolution because of large numbers of stations contributing data; however, the majority of stations may be clustered within high population regions whereas other areas of a cell, grid, or region are grossly underrepresented. Recent improvements in the field of climate downscaling have produced spatial temperature mapping tools such as PRISM (Parameter Regression on Independent Slopes Model) and DAYMET, which output roughly one kilometer (km) spatial resolution; however, accounting for small-scale spatial and temporal temperature variability in complex terrain is still tenuous and lacks reliable inference power for ecological variables (Holden et al., 2011).

A number of studies focused on the improvement of downscaled models and gridded datasets for mountain regions highlight that models should integrate topography and elevation effects on surface temperatures and precipitation (Daly, 2006; Daly et al., 2002; Daly et al., 2008; Giorgi et al., 1997; Lookingbill and Urban, 2003; Stahl et al., 2006). The importance of topographic complexity and elevation is exemplified in their effects on dictating site-specific climatic and ecological gradients/zones, localized surface flow patterns such as uplift and cold air drainage, and the presence of seasonal inversions (Lookingbill and Urban, 2003; Daly, 2006). Further, the proximity to water bodies exerts controls on

local climate and precipitation patterns. Montane temperatures in coastal maritime regions may be affected by unique wind and moisture patterns, or be affected by lentic or riparian zones, both of which are not accounted for by current models, at least at the scales needed to inform ecological research (Daly, 2006). Current efforts to increase the reliability of spatially interpolated climate patterns have attempted to account for topographic and elevational complexity by incorporating weighted temperatures based on elevation. While the inclusion of a weighted elevation signal within GCM and temperature prediction models can certainly improve their accuracy and effectiveness (e.g., Daly et al., 2002; Wang et al., 2012), the high variability of the temperature-elevation signal across temporal and geographic scales presents an ongoing challenge for spatial interpolation of climate in regions with complex terrain (Stahl et al., 2006). For example, differences in slope and aspect are often negated (even in a model that incorporates an elevation signal) and the dichotomy between amounts of solar radiation received on separate aspects can precipitate wholly separate thermal gradients and regimes (Lookingbill and Urban, 2003).

A second improvement to current climate studies in mountainous regions is an effort to mitigate sparse station sampling by the use of portable temperature loggers. These store-on-board devices can be purchased relatively cheaply and can increase an investigator's capability for high-density sampling and subsequent downscaled analysis. As the most commonly used portable temperature loggers from Onset Computer Corp. (HOBO), OnSolution Pty. Ltd. (Thermochron), and Campbell Scientific can be set to record temperature at intervals ranging from minutes to days, these instruments provide a valuable opportunity to capture the inherent variability of temperature across temporal scales. Indeed, the use of portable data loggers for various environmental applications has been widely accepted as an effective alternative to commercially available weather stations, when attempting to bolster both sampling capability and sampling resolution (Chaput and Gajewski, 2014; Clark et al., 2006; Gardner et al., 2009; Holden and Jolly, 2011; Hubbart et al., 2005; Hubbart et al., 2007; Lookingbill and Urban, 2003; Lundquist et al., 2007). A concern, however, with regard to the use of these devices, is the potential for biased measurements due to exposure of the thermistor to solar radiation.

Just as expensive meteorological stations contain a thermistor that is shielded and regulated for sunlight exposure, radiation shields must also be used in concert with portable temperature loggers to insure the accuracy of the portable device (Clark et al., 2006; Hubbart, 2011; Lin et al., 2001; Lundquist and Huggett, 2008; Richardson et al., 1999; Tarara and Hoheisel, 2007). Heating of a portable logger and subsequent temperature reading bias may not only occur as a result of direct solar radiation exposure, but additionally, sensors must be shielded from indirect solar exposure reflected from the ground surface (Huwald et al., 2009). Common and effective shield designs have been rigorously tested and generally take the form of a stacked, muli-plate Gill shield design, or a series of inverted funnels (Hubbart, 2011; Richardson et al., 1999; Tarara and Hoheisel, 2007). Further, recent field testing by Lundquist and

Huggett (2008) demonstrated that deploying sensors within stands of conifer trees was an overwhelmingly effective method of reducing solar radiation-induced bias. If effective solar shielding is applied to portable temperature loggers, they offer a useful means to improve climate monitoring in complex terrain by ameliorating the economic and logistic difficulties owed to employing high-end meteorological stations.

3.1.3 – Lapse Rates of Air Temperature

Climate in complex terrain is reported, investigated, and modeled using the temperature proxy, as both surface and atmospheric temperatures have been overwhelmingly described to be the most critical variables relative to hydrological, ecological, and climatic dynamics (Blandford et al., 2008; Dobrowski et al., 2009; Li et al., 2013; Lookingbill and Urban, 2003; Minder et al., 2010). It has been widely described that spatial and temporal temperature trends in mountainous regions demonstrate a coupling with elevation/altitude (e.g., Blandford et al., 2008; Mountain Research Initiative, 2015). This coupling is generally defined as a lapse rate, whereby, air temperature generally decreases at some determinable increment with increasing elevation or altitude.

Lapse rates, being the general decrease of air temperature with increasing elevation or altitude are reported with a large amount of variation as to the distinct definition of the temperature-elevation relationship. Herein, a disentanglement of the generalized term is required in order to explicate the various underlying processes affecting lapse rates, and resolve inconsistencies in both the literature and climate science in general. As all the following definitions may be reported in the literature simply as "lapse rates", specificity with regard to particular definitions is paramount. The first critical distinction must be made between lapse rates of "free-air" within the atmosphere and lapse rates of air temperature near the Earth's surface; hereafter, referred to as near-surface lapse rates. Free-air temperatures have been established as, "temperatures in the free atmosphere that are not substantially influenced by surface boundary layer effects" (Pepin and Seidel, 2005). Air that is influenced by the surface boundary layer is considered "near-surface". A second critical distinction must be made in terms of the characterization of saturation level for the air itself, in that lapse rates may refer to either moist adiabatic or dry adiabatic conditions. As a warm air mass expands and, as a result, rises in altitude, its temperature correspondingly decreases, as does its pressure (Dodson and Marks, 1997). Of note is that contact by an air mass with complex terrain can induce this process (with the same result), defined as orographic uplift (Dodson and Marks, 1997). During the process of vertical movement, only if no thermal energy is transferred into, or out of the system, the inherent rate of air temperature decrease is called adiabatic (Dodson and Marks, 1997). A distinction can now be made between lapse rates of saturated and non-saturated air, thus, the moist adiabatic lapse rate and dry adiabatic lapse rate. A third critical distinction involves a clarification

of averaging terminology precipitated by the fact that rarely could a lapse rate ever be totally adiabatic (Dodson and Marks, 1997). Thus, when decreases of temperature per unit elevational or altitudinal increase are measured for a region across an established temporal scale, for free-air or otherwise, that decrease can be referred to as an atmospheric or environmental lapse rate (Dodson and Marks, 1997). Again though, the terms "atmospheric" and "environmental" lapse rates are seemingly used interchangeably, though they may refer to any vertical column or gradient of the atmosphere, whether it be surface boundary layer-influenced, or otherwise (Blandford et al., 2008; Dial et al., 2015; Dodson and Marks, 1997; Dobrowski et al., 2009; Gardner et al., 2009). Additionally, atmospheric/environmental lapse rates generally concern averages or mean temperature-elevation trends. When the inclusion of the descriptor "standard" is used in conjunction with atmospheric and/or environmental lapse rates, this terminology refers to the standard atmosphere unit of pressure, and further would assume the lapse rate was calculated in terms of the global mean pressure at sea level (which equals 1 atmosphere (atm) = 101.325 kilopascals (kPa) = 1013.25 millibars (mbar)). In other words, the standard atmospheric and/or environmental lapse rate is the global mean lapse rate as determined by a global mean air pressure at sea level. Finally, a distinction must be clarified as to the directional trend of a lapse rate. The suite of climate literature on lapse rates uses varying terminology to describe a lapse rate's value including descriptors such as: positive, negative, strong, weak, steep, shallow, increasing, or decreasing. Often, there have been opposite definitions of the same word demonstrated within the literature. Herein, I follow the convention of Blandford et al. (2008) in defining higher values of a lapse (i.e., more negative) to coincide with descriptors like strong, steep, or increased. Therefore, steeper lapse rates in this study indicate a more rapid, more negative, and higher absolute value decrease of temperature with increasing elevation. As Gardner et al., (2009) note, many glaciology publications adopt the opposite convention. Ergo, the lapse rate values reported in my study should be interpreted with caution when comparing these results to other systems. Specific values of the aforementioned lapse rate types are subsequently described below with special attention paid to the behavioral differences between free-air and near-surface lapse rates.

Reported regional lapse rates and mean environmental lapses vary within the literature; however, certain values are described as the generally accepted averages across lapse rate types. The most commonly cited lapse rate by far, is the mean environmental lapse rate, which is also interpreted as both the global mean free-air and near-surface lapse rate. This average lapse rate is generally listed as being between -6.0°C km^{-1} and -6.5°C km^{-1} (Blandford et al., 2008; Courault and Monestiez, 1999; Dial et al., 2015; Dobrowski et al., 2009; Dodson and Marks, 1997; Gardner et al., 2009; Harlow et al., 2004; Lookingbill and Urban, 2003; Li et al., 2013; Lundquist and Cayan, 2007; Marshall et al., 2007; Roe and O'Neal, 2009; Rolland, 2003; Scally, 1997; Stahl et al., 2006; Wang et al., 2011). The generic dry adiabatic environmental lapse rate is given as -9.8°C km^{-1} (Blandford et al., 2008; Dial et al., 2015;

Dobrowski et al., 2009; Dodson and Marks, 1997; Rolland, 2003). For saturated air, the generic moist adiabatic environmental lapse rate is given as -4.0°C km^{-1} (Blandford et al., 2008; Dodson and Marks, 1997; Rolland, 2003).

Though the mean environmental lapse rate has been used in spatial interpolation modeling of air temperatures (e.g., Courault and Monestiez, 1999; Dodson and Marks, 1997), lapse rates have been overwhelmingly shown to strongly vary across several axes including spatial, temporal, and physiographic scales, as well as by synoptic weather pattern type. Consequently, it is generally recommended that investigators abandon or use extreme caution when using the average environmental lapse rate, as it is ineffective for studies requiring high-precision estimations and temperature extrapolations for localized hydrologic, ecologic, or climatic investigations (Blandford et al., 2008; Lundquist and Cayan, 2007; Rolland, 2003; Scally, 1997). Lapse rates of free-air are significantly less variable than near-surface lapse rates (e.g., Blandford et al., 2008; Harlow et al., 2004), and the aforementioned spatial, temporal, and physiographic-scale differences of near-surfaces warrant that they be used in favor of free-air rates, when studies concerning the terrestrial environment are involved (including hydrology). Henceforth, I specify that the subsequent discussion of lapse rate behavior is relegated to near-surface lapse rates. This designation additionally applies to subsequent lapse rate measurements and analyses conducted herein.

Near-surface lapse rates have been widely described to vary across temporal scales, with said variability occurring over daily, monthly, annual, and seasonal time steps (Blandford et al., 2008; Bolstad et al., 1998; Dial et al., 2015; Dobrowski et al., 2009; Gardner et al., 2009; Gouvas et al., 2011; Harlow et al., 2004; Kattel et al., 2013; Li et al., 2013; Lundquist and Cayan, 2007; Marshall et al., 2007; Minder et al., 2010; Pepin, 2001; Pepin and Losleben, 2002; Pepin et al., 1999; Rolland, 2003; Stahl et al., 2006a; Wang et al., 2011). Often, seasonal and inter-annual differences in the amount of solar radiation received by a region and local weather types affects lapse rates, causing them to demonstrate variability across temporal scales. For example, in the central Sierra Nevada, near-surface lapse rates measured from daily mean temperatures between 2002 and 2004 varied between -0.23 and -1.02°C $100m^{-1}$ on a given day with a root-mean square error of 1.70°C. Wang et al. (2011) contrasted average near-surface lapse rates calculated from monthly mean temperatures between 1961 and 2003 on the Tibetan Plateau. In July, the average lapse rate measured -0.39°C $100m^{-1}$, while the mean January lapse rate measured 0.25°C $100m^{-1}$ (Wang et al., 2011). In the Canadian high Arctic, lapse rates measured from mean daily temperatures between 1988-2007 ranged from a low of 1.19°C $100m^{-1}$ to a high of -1.48°C $100m^{-1}$, with respective (and variable) monthly mean lapse rate values generally being 0.18°C $100m^{-1}$ greater in the summer than in the winter (Gardner et al., 2009). Monthly mean lapse rates measured in Greece were reported to be markedly greater in summer and, across months, ranged from -0.62 to -0.92°C $100m^{-1}$ (Gouvas et al., 2011).

Similarly, differing mean lapse rate estimations for each month of a year have been described in: south-central Idaho, USA (Blandford et al., 2008), Ellesmere Island, Canada (Marshall et al., 2007), the Cascade Range, USA (Minder et al., 2010), the Italian and Austrian Alps (Rolland, 2003), the Colorado Rockies, USA (Pepin and Losleben, 2002), northern England (Pepin, 2001), the Nepal Himalaya (Kattel et al., 2013), the southern Appalachian Mountains, USA (Bolstad et al., 1998), and mainland China (Li et al., 2013). All studies in the aforementioned examples described general trends of steepening lapse rates in summer and shallower lapse rates during winter months. This seasonal differentiation of lapse rates is often attributable to lapses being weakened during the winter months, whereby on cold, clear nights channeled air flow and cold air pooling causes inversions of air temperature (Gustavsson et al., 1998). This occurrence often reverses the lapse rate (or at least greatly lowers it), resulting in variable temporal lapses ranging from daily/diurnal scales (e.g., Blandford et al., 2008; Marshall et al., 2007; Pepin and Losleben, 2002), to inter-annual monthly scales (e.g., Kattel et al., 2013; Rolland, 2003), and further, intra-annual scales (e.g., Li et al., 2013). Generally though, across the time series of a given year, a differential in the radiative heat input/flux and convection of a region acts as a key driver of both temporal near-surface temperature, and lapse rate variability (Kattel et al., 2013; Li et al., 2013; Pepin and Losleben, 2002).

In addition to lapse rate variability across temporal scales, lapse rate behavior varies spatially due to topographic and landscape physiographic effects. Dobrowski et al. (2009) exemplified spatial differentiation of temperatures in complex terrain by measuring the effects of landscape physiography and topoclimate in the Lake Tahoe region between 1995 and 2006. Findings note that 70-80% of near-surface temperature variability was explained by regional/local conditions, and the remaining variance could be explained by spatial differences in temperature attributed to physiographic features (Dobowski et al., 2009). Additional research of near-surface lapse rates in the Sierra Nevada by Lundquist and Cayan (2007) demonstrated marked differences in near-surface temperatures on west-facing versus east-facing slopes. As previously mentioned, spatial orientation and topographic complexity (which are unique to any given region), govern the directional flow of near-surface air masses, and also explain the presence and prominence of inversion effects (e.g., Kattel et al., 2013). As such, spatial lapse rate variability is intuitive; in that complex terrain features receive variable amounts of radiant energy, have unique elevational gradients, and unique proximal physiographic features such as water bodies, ice, or barriers to air flow (Stahl et al., 2006a). Indeed, the conglomerate of continentality, topography, and latitude will affect diurnal temperature variation, cloud and precipitation regimes, local radiative input, and slope-aspect-level differentiation of local climates, and the lapse rates therein (Barry, 1992; Tang and Fang, 2006). This spatial differential in localized lapse rate values has been described as especially prominent in winter (due to local inversions); however, spatial variability is generally present across all spatial scales

over the course of a given year. For example, lapse rates measured on mainland China and the Tibetan plateau across all seasons demonstrated a stratified distribution, spanning from southeast to northwest with respective values of 0.30 – 0.90°C $100m^{-1}$ (Li et al., 2013). Moreover, other studies from the Tibetan Plateau suggest that lapse rates change with both latitude and longitude, underscoring the spatial drivers of lapse rate variability (Du et al., 2010). Similar regional distributional uniqueness of lapse rates was found across the Alps in Europe including regions in France, Switzerland, Italy, and Austria (Rolland, 2003). In North America, research from the Washington Cascades revealed consistent spatial differences in lapse rate variability between windward (~0.40°C $100m^{-1}$) and leeward- (~0.10°C $100m^{-1}$) facing slopes (Minder et al., 2010). Likewise, in eastern China, lapse rates were shown to be markedly different on south versus north-facing slopes (Tang and Fang, 2006). In the Oregon Cascades, calculated/estimated lapse rates were shown to be greatly improved by including relative slope position as an explanatory variable in the statistical modeling approach (Lookingbill and Urban, 2003). Indeed, it is this widely described spatial climate variability that precipitated the need within the scientific community to derive spatial climate models that account for regional differences in climate. Daly et al. (2008) substantiates that both terrain and local landscape physiography considerations are paramount to improving gridded climate models such as PRISM.

The third axis of lapse rate variability is defined by regional differences in synoptic weather type. Again, this is intuitive when considering the ideal gas law, as respective local weather systems contain inherently different states of air pressure. Lapse rates measured in northern England (Pepin et al., 1999) were steeper during conditions of both high solar radiative input and high winds. Conversely, synoptic weather conditions characterized by calm winds, moist air, and south-flowing air masses produced much weaker lapse rates within the same region (Pepin et al., 1999). Interestingly, a somewhat opposite trend was described by Stahl et al. (2006a), in that lapse rates in British Columbia, Canada increased during synoptic conditions characterized by low-pressure systems that produced high precipitation and west/southwest directional air-flows. In south-central Idaho, Blandford et al. (2008) explored lapse rate variability across synoptic scales and found consistently steeper lapse rates during dry conditions, and conversely, substantially weaker lapse rates during moist conditions. Summer conditions in the northern hemisphere are marked by high surface heating and this, in turn, can cause convergence onto a characteristic dry-adiabatic lapse rate (Blandford et al., 2008; Pepin et al., 1999). In the Kluane region of British Columbia, Canada, temperature measurements for a vast region encompassing a 400-m elevational gradient across 3° of latitude were strikingly similar and demonstrated a marked dependency of near-surface temperatures according to synoptic weather type (Chaput and Gajewski, 2014). The authors note that large weather systems (>100 km in size) seemingly exert stronger control over regional near-surface temperatures than other forcings (Chaput and Gajewski, 2014). Though several authors have reported

differing lapse rate trends based on synoptic weather type, the general consensus remains that lapse rates are weaker in moist and/or cool conditions, while they tend to steepen during dry and/or warm conditions (Blandford et al., 2008; Kattel et al., 2013; Li et al., 2013; Minder et al., 2010; Pepin, 2001; Tang and Fang, 2006). This trend is attributable to water vapor condensation that produces increased latent heat release by humid air (Kattel et al., 2013; Li et al., 2013). Surface temperatures are thus decreased by moist air or during periods of heavy rainfall, subsequently reducing the temperature-elevation differential. Also of note is that conditions of heavy clouds also reduce surface heating and reduce near-surface lapse rates (Kattel et al., 2013). When conditions in complex terrain are devoid of ambient moist-air-cooling (i.e., are dry and warm), a steeper temperature-elevation gradient generally prevails.

In summary, lapse rate behavior is determined by the nexus of temporal, spatial, and synoptic condition variability. Further, these axes are seldom mutually exclusive. Synthesis of the current literature highlights that the uniqueness of near-surface lapse rates measured in a wide array of regions across the globe warrants the abandonment of a standard environmental lapse rate as a reliable estimation of temperature at elevation for any given region. Moreover, the use of a global mean environmental lapse rate as a metric within global circulation models and gridded downscaled climate prediction models is tenuous and may vastly under- or over-estimate temperature decrease with elevational increase for a region. This fact presents one of the most important fundamental flaws in current climate modeling and projection efforts. The preponderance of current scientific studies that aim to estimate the effects of climate warming on hydrological and biophysical systems in mountainous regions unequivocally require accurate and local-scale measurement of near-surface lapse rates.

3.2 – The Scope of Ungulate Ecology and Climate Change

The future implications of climate change represent a fundamental concern within the scientific community. Increased climate warming has resulted in ecological change and is of notable concern. Studies have shown that changing climatic regimes can affect the geographic range, distribution, survival, and population dynamics of species, as well as ecosystem function and phenology across various systems (Albon and Langvatn, 1992; Foley et al., 2000; Lawler et al., 2009; Mawdsley et al., 2009; McCarty, 2001; Mysterud et al., 2001). High-resolution data are of considerable importance to ecological conservation to make informed management decisions regarding the fate of species as they respond to increasing climate warming (Mawdsley et al., 2009). At higher latitudes in particular, climate change may be more extreme (Serreze and Barry, 2011). Thus, study of climate effects on ecosystems and the species therein is particularly imperative for ecological communities in Alaska. Further, in mountainous regions, complex terrain may amplify climate variability and this underscores the need to study the ecological implications of climate change in Alaska (Blandford et al., 2008; Rolland, 2003; Scally, 1997; Wang et

al., 2012a). For example, variation in alpine plant species abundance, nutritional quality, and phenology can all be affected by climatic variation and exert fundamental effects on the ecology of many North American herbivores (Bischof et al., 2012; Fox, 1991; Lenart et al., 2002). Additionally, the rate at which snow melts at alpine sites influences the persistence of high-quality forage resources throughout the summer (Bischof et al., 2012; Fox, 1991). When persistent summer snow is limited, forage nutritional quality decreases (e.g., crude protein content) across the landscape as a result of increased cell lignification (Bo and Hjeljord, 1991; Fox, 1991; Lenart, et al., 2002). Moreover, Lenart et al. (2002) describe that cloudy summers translate to an increase in available nitrogen in certain alpine forages, as compared to sunny summers. As such, the ability for ungulates to adequately obtain sufficient nutritional resources in preparation for fall breeding and winter survival may be hindered in warmer years (White et al., 2011).

In addition to considerations of climatic effects on the quality of available forage (Giacometti et al., 2002), other aspects of ungulate ecology can be influenced by thermal changes such as: homeothermic maintenance (e.g., Natori and Porter, 2007), predator avoidance (e.g., Hamel and Côté, 2007; Rachlow and Bowyer, 1994), and habitat selection (e.g., Bowyer et al., 1998; Grignolio et al., 2004, 2007). Differences in both the life-history strategies of sexually segregated mammals and behavior (e.g., Aublet et al., 2009) are also factors that may be affected by climate warming across spatial and/or temporal scales (Kie, 1999). In order to properly manage and conserve ungulates and the systems they inhabit, it is necessary to understand the complex interactions between the aforementioned ecological factors. Trade-offs may occur between two or more factors to maximize fitness and/or survival. For example, Bowyer et al. (1998a) investigated trade-offs in habitat selection in black-tailed deer (*Odocoileus hemoinus columbianus*) and noted that lactating females selected habitats with higher nutritional forage and thermal regimes that allowed for the reduction of heat stress rather than sites with minimal predation risk. Conversely, Festa-Bianchet (1988) demonstrated that bighorn sheep (*Ovis canadensis*) trade-off high quality nutritional forage for predator avoidance during lambing. Likewise, Grignolio et al. (2007) demonstrate similar findings in alpine ibex (*Capra ibex*) as females with kids traded high-quality forage for low-predation-risk sites until offspring were of sufficient size (at which point the mother and kid would return to higher quality forage sites). Such trade-offs between forage availability and predator avoidance are common in alpine ungulates and have also been reported in Dall's sheep (*Ovis Dalli*) (Rachlow and Bowyer, 1994) and mountain goats (*Oreamnos americanus*) (Hamel and Côté, 2007). These examples demonstrate the enigmatic relationship between resource selection and physiological limits associated with life-history needs like reproduction and predator avoidance. Within ungulate ecology as a whole, differences in trade-offs and selection appear to be as widely varied as the life history strategies observed among the myriad of species. This inconsistency in selection and trade-offs in

ungulates emphasizes the need for further study of the drivers and consequences of life-history characteristics. Furthermore, the existence of trade-offs engenders compelling questions about the implications of shifting states of ecosystems under climate warming scenarios.

As herbivores, ungulates are especially linked to air temperature effects on plant phenology because their survival is determinant upon meeting adequate nutritional demands. Most often, ungulates annually migrate from winter to summer ranges following the rate of green-up, as newly emerged forage plants are most nutritious (Bischof et al., 2012). Phenological green-up is, of course, a consequence of temporal and spatial thermal gradients. In mountainous areas especially, air temperature lapse rates (an incremental decrease of temperature with increasing elevation) govern snow persistence along elevational gradients during the onset of summer. As snowline abates in spring, highly nutritious plant emergence takes place at the melt terminus and this trend temporally continues upslope until snow is no longer present in summer. Although Bischof et al. (2012) found differences in space-use tactics with regard to resident and migratory red deer (*Cervus elaphus*), both groups demonstrated "the pursuit of spring", either migrating along a spatial gradient of phonological green-up or augmenting season-long habitat use to access the highest nutritional plant growth. In addition to improving the explanatory power of space-use and habitat selection in ungulates, lapse rates are also a useful consideration that aids investigators in predicting overall range potential for a sensitive ungulate species, based on metabolic and energetic demands (W. Porter – UW Madison Dept. of Zoology, pers. comm.). Natori and Porter (2007) demonstrated that a mechanistic energetics model accurately predicted the winter and summer ranges of a thermally sensitive (IUCN) threatened ungulate, the Japanese serow (*Capricornus crispus*). This research was a novel step forward in synthesizing the nexus between physiological demands, habitat use, and spatial-thermal gradients.

The advent of mammalian energetics modeling in recent years has served to highlight the aforementioned critical linkage between ungulate ecology and climate change; in that ungulates primarily ameliorate thermal sensitivity by way of a behavioral response, or shift in activity pattern. For example, an investigation of activity budgets for steenbok (*Raphicerus campestris*), impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), and giraffe (*Giraffa camelopardalis*), revealed that all species reduced time spent moving and feeding while increasing the amount of time spent standing or resting on hot days (Du Toit and Yetman, 2005). This pattern was especially prevalent for the larger-bodied ungulates (Du Toit and Yetman, 2005). In another example, a study of moose (*Alces alces*) similarly found that the animals reduce their activity on warm days (Van Beest and Milner, 2013). Moose that selected for shaded habitats during periods of thermal stress and high quality forage habitats under cool temperature regimes, lost less body mass over the course of a year than their alternately behaving counterparts (Van Beest and Milner, 2013). Nutritional condition as an effect of climate has also been

described in elk (*Cervus elaphus*; Long et al., 2013). A comparison study of elk populations living in two distinct habitat types revealed animals inhabiting more forested regions did not trade off thermoregulatory behavior for optimum foraging behavior, whereas animals inhabiting an unforested region commonly engaged in thermal stress reduction behavior in lieu of foraging (Long et al., 2013). Indeed, behavioral shifts in ungulates due to thermoregulatory need have been described in a wide variety of ungulate species (Table 1).

Author(s)	Species	Behavioral Shift Described
Fox 1978	mountain goat (*Oreamnos americanus*)	Altitudinal movement and reduced midday activity
Parker and Robins 1984	mule deer (*Odocoileus hemionus*)	Increased respiratory rate and open-mouth panting
Parker and Robbins 1984	elk (*Cervus elaphus*)	Increased respiratory rate and open-mouth panting
Maloney et al. 2005	black wildebeest (*Connochaetes gnou*)	Shift to nighttime feeding
Seip and Bunnel 1985	stone's sheep (*Ovis dalli sonei*)	Altering habitat selection
Schwab and Pitt 1991	moose (*Alces alces*)	Altering habitat selection
Roberts and Dunbar 1991	mountain reedbuck (*Redunca fulvorufula*)	Reduced midday activity and increased diurnal activity
Owen-Smith 1994	greater kudu (*Tragelaphus stepsiceros*)	Reduced overall activity
Natori and Porter 2007	Japanese serow (*Capricornus crispus*)	Alteration of spatial distribution and habitat use
Hamel and Côté 2008	mountain goat (*Oreamnos americanus*)	Reducing daily forage time to evening
Aublet et al. 2009	alpine ibex (*Capra ibex*)	Increased use of high altitude habitats
Van Beest and Milner 2013	moose (*Alces alces*)	Selection of mature forest habitats

Table 1. Literature examples of behavioral shifts due to temperature in ungulates

In the most general sense, ungulate species passively thermoregulate on warm days by spending less time active, often reserving energetic expenditures to cooler periods of day (e.g., early morning and evening) (Du Toit and Yetmen, 2005; Hamel and Côté, 2008; Owen-Smith, 1994; Roberts and Dunbar, 1991). Micro-site habitat selection also occurs as a thermoregulatory strategy though. For example, Schwab and Pitt (1991) describe moose bedding in coniferous forest in order to maintain a stable core body temperature when faced with heat stress. In the case of alpine ungulates however, canopy cover may be sparse or may not be in close enough proximity to escape terrain (and/or foraging sites) to act as a passive thermoregulatory mechanism. A study of alpine ibex in the Italian Alps describe daily altitudinal movement as a thermoregulatory strategy used to take advantage of cooler temperature regimes at higher elevation sites (Aublet et al., 2009). Use of such thermoregulatory strategies may represent a trade-off and

result in reduced time spent actively foraging. These examples demonstrate novel approaches to evaluating the effects of globally warming temperatures, in that direct behavioral or body condition evidence can be used to signal changes in biological communities, rather than inferences using indirect climate change indicators (e.g., plant phenology).

Research within this field has repeatedly illuminated how ungulates serve as ecosystem indicator species through their multifaceted dependence on localized thermal regimes and sensitivity to changes therein. Current ungulate research suggests climate change signals from these animals are a consistent and mostly ubiquitous phenomenon globally. For example, the Nilgiri tahr (*Nilgiritragus hylocrius*), a montane ungulate endemic to the Western Ghats of India, experienced a 75% reduction in population size within parts of its range between 1975 and 1991 (Sukumar et al., 1995). Climate change induced shifts in near-surface thermal regimes within tahrs' range are thought to be the primary driver of montane grassland disappearance that poses a substantial risk of extinction for this species (Sukumar et al., 1995). In Alaska, White et al. (2011) note that the prevalence of warm days in summer results in lower mountain goat survival the following winter, most likely because of an insufficient procurement of nutritional resources. In the Alps, research notes substantial temporal trends in the reduction of body mass for populations of alpine chamois (*Rupicapra rupicapra*) (Mason et al., 2014). Rather than the prevalence or phenology of forage resources, chamois body mass seems to have declined over a nearly 30 year span due to increased thermal stress-induced reductions in foraging behavior (Mason et al., 2014). Interestingly, alpine ungulates above all others epitomize the importance of considering lapse rates as a key factor in climate-driven ecosystem change research. This notion is a function of recent observations that mountain-inhabiting domestic sheep (*Ovis aries*), alpine chamois, and alpine ibex all demonstrate the notable thermoregulatory behavior of altitudinal movement when faced with warm ambient temperatures (Aublet et al., 2009; Mason et al., 2014). In effect, the animals are taking advantage of near-surface lapse rates as a strategy to maintain a stable core body temperature. Though investigators can, and have measured the distance upslope that these alpine ungulates may migrate on warm days, predicting an elevational contraction of range based on warming scenarios may overgeneralize faunal reactions of thermal shift. A clear understanding of regional lapse rates coupled with these investigations remains imperative to robustly describing wildlife as indicators of climate change.

Findings in the aforementioned studies exhaustively underscore the need to understand the effects of climate warming on ungulate behavior. For mountain ungulates in Alaska, there is sparse information on the potential effect of a warming climate as a constraint on various behaviors (but see Fox, 1978). Similar to alpine ibex (an ecologically equivalent species in niche and phenotype), mountain goats may exhibit similar patterns of thermoregulation and altitudinal movements. This behavior has, as of yet, not been explicitly described. Species-specific strategies such as the use of shady micro-sites may prevail due

to differences in the evolution of a behavioral phenotype. Other factors such as distance to escape terrain or available forage within Alaska mountain goat habitat could influence the behavior of this ungulate in ways unique to the species. The combined findings of Hamel and Côté (2008) and White et al. (2011) that mountain goats spend less time foraging on warm days and mountain goat survival is lower following warm summers imply that climate can affect critical aspects of mountain goat fitness such as foraging, not just through direct ecological impacts in alpine environments but through a thermoregulatory behavior mechanism as well. Further, previous studies by Hamel and Côté (2008) and Aublet et al. (2009) (though robust to their objectives) utilized sparse weather station data to incorporate temperature in to their analysis (n=1 station). This additionally emphasizes the need to conduct a thermoregulatory behavior study in conjunction with high-resolution temperature monitoring. This effort not only contributes to the understanding of foraging ecology and eco-physiology of this species, but will also allow for informed management planning with regard to impending climate warming.

Chapter 4 – Study Area

4.1 – Description of Southeast Alaska and Berners Bay

I investigated mountain goat behavior-temperature relationships in Southeast Alaska (Alaska Panhandle; Figure 1).

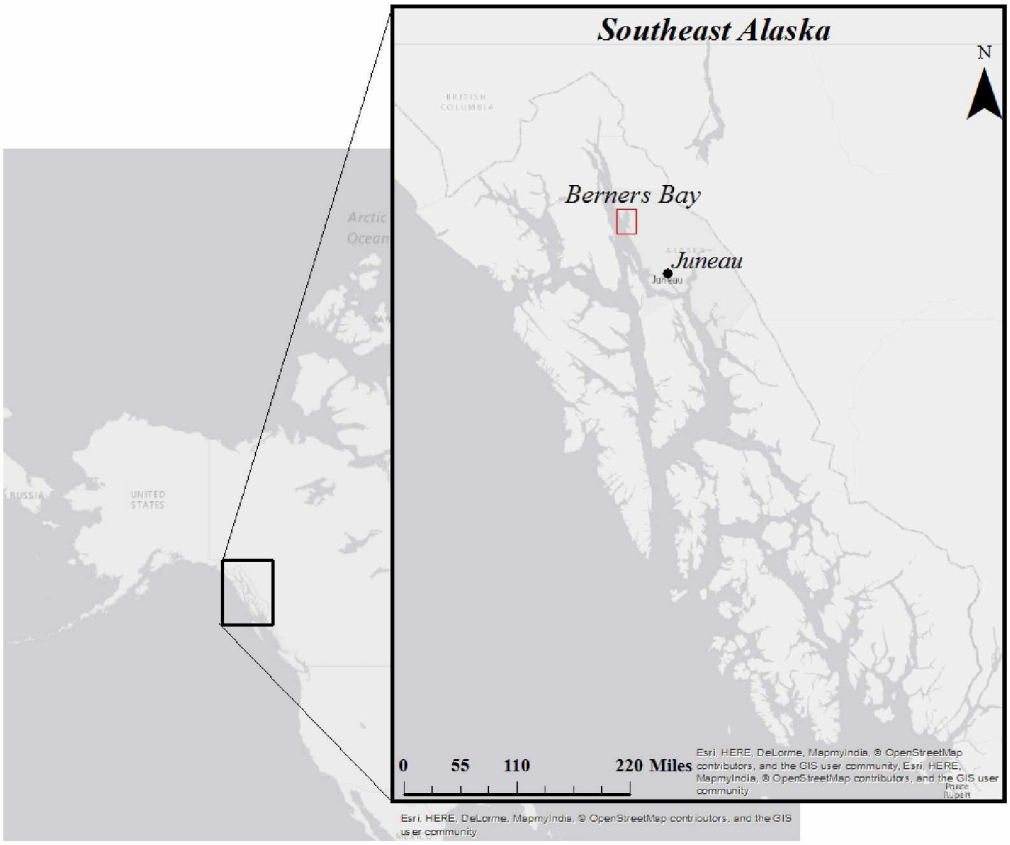

Figure 1. Study area in Berners Bay, Southeast Alaska

Defined as the pacific coastal temperate rainforest ecoregion, my study area is characterized by an array of climatological, topographical, and ecological complexity. The majority of the land in Southeast Alaska is part of the 6.8 million hectare (ha) Tongass National Forest. Southeast Alaska's climate is generally characterized as maritime: abundant in precipitation, with mild winters and cool summers. Day lengths in this region vary from 6 hours in the winter, to 18 hours in the summer. Seasonality in this region is characterized by a long winter (~9 months) with a short summer (~3 months). The Panhandle is climatically influenced by the warm-water (>3.9˚C) Alaska Current, which forms a large gyre in the Gulf

of Alaska as a portion of the North Pacific current is forced northward by northwestern North America (Schoen and Dovichin, 2007). Mean annual temperature, precipitation, and precipitation falling as snow are: 5.6˚C, 1473.2 millimeters (mm), and 2362.2mm, respectively (Kelly et al., 2007). The region is topographically and climatologically influenced by thousands of tidewater and alpine hanging glaciers, as well as inland ice fields. This glacial activity shaped the mountainous landscape of this region such that any land-based location within Southeast Alaska is no more than 48km from saltwater (Schoen and Dovichin, 2007).

My specific study area, Berners Bay, is located approximately 72km north of Juneau, AK. Berners Bay runs north/south for approximately 20km. Berners Bay and the greater Juneau area are highly mountainous and surrounded to the east by North America's fifth-largest ice field. It includes 1,500 sq. mi. of ice that arcs around the mountains east of Lynn Canal and empties into various estuarine systems via 38 glaciers (Kelly et al., 2007; Sprenke et al., 1999). The greater Berners Bay area was of particular interest for my research, as it is a microcosm of greater Southeast with nearly all environmental and ecological zones represented in this complex and highly productive region.

Mountain goats generally remain obligates of both the subalpine meadow and alpine zones in summer (Figure 2).

Figure 2. Mountain goats in Berners Bay, Alaska. Female mountain goat with kid (left) and male mountain goat (right). Photos: Jeffrey Frederick

The animals generally remain in close proximity to steep or cliffy terrain as a predator avoidance strategy. Potential predators in my study area include wolves (*Canus lupis*), brown bears (*Ursus arctos*), black bears (*Ursus americanus*), wolverines (*Gulo gulo*), bald eagles (*Haliaeetus leucocephalus*), and golden eagles (*Aquila chrysaetos*) (Fox et al., 1989; White et al., 2012). Common sub-alpine floral species in

Berners Bay include sedges (*Carex* spp.), lupin (*Lupinus nootkatensis*), fireweed (*Chamerion angustifolium*), cow parsnip (*Heracleum maximum*), and lady fern (*Athyrium filix-femina*). Preferred mountain goat forage within this zone include deer cabbage (*Nephrophyllidium crista-galli*), alpine sagewort (*Artemesia arctica)*, broadleaf arnica (*Arnica latifolia*), lutkea (*Luetkea pectinate*), and most importantly/preferred, long-awned sedge (*Carex macrochaeta*) (Fox et al., 1989). Krummholtz often predominate on the periphery of the herbaceous meadows in craggier, less saturated areas.

Chapter 5 – Methods

5.1 – Lapse Rate Monitoring

5.1.1 – Thermistor Instrumentation

Near surface air temperatures were measured using HOBO TidbiT v2 temperature loggers (Onset Computer Corp., model: UTBI-001) (Figure 3).

Figure 3. HOBO TidbiT v2 temperature logger, *Photo courtesy of Onset*

These waterproof, store-on-board thermistors are portable (3×4cm), and have an accuracy of ±0.2°C. Each logger used in this study was calibrated and accuracy tested by programming the loggers to record temperature every 10 minutes and placing loggers in a controlled 0°C ice bath for one hour. Any logger that did not read within ±0.2°C of the ice bath temperature during the test sampling period was not used in this study. Subsequent to accuracy testing, sensors were prepared for deployment in the field by programing the logger to record measurements of temperature in °C every one hour. Data from the loggers were retrieved by fitting a sensor-specific coupler to a HOBO waterproof shuttle (Onset Computer Corp., model: U-DTW-1). Temperature measurements were then downloaded and processed using HOBOware Pro Software (Onset Computer Corp., model: BHW-PRO-CD).

5.1.2 – Sensor Deployment

As near surface lapse rates are often measured and reported in °C $100m^{-1}$, I deployed temperature sensors in an array composed of transects of sensors spaced at 100m elevational intervals from sea level to site apex (e.g., "mountain top"). As the aspect of a slope may contribute to localized differences in thermal regimes (Kattel et al., 2013; Minder et al., 2010; Rolland, 2003; Schoen and Dovichin, 2007; Tang and Fang, 2006), the location of transects were chosen to represent a north-, south-, east-, and west-facing aspect (Figure 4).

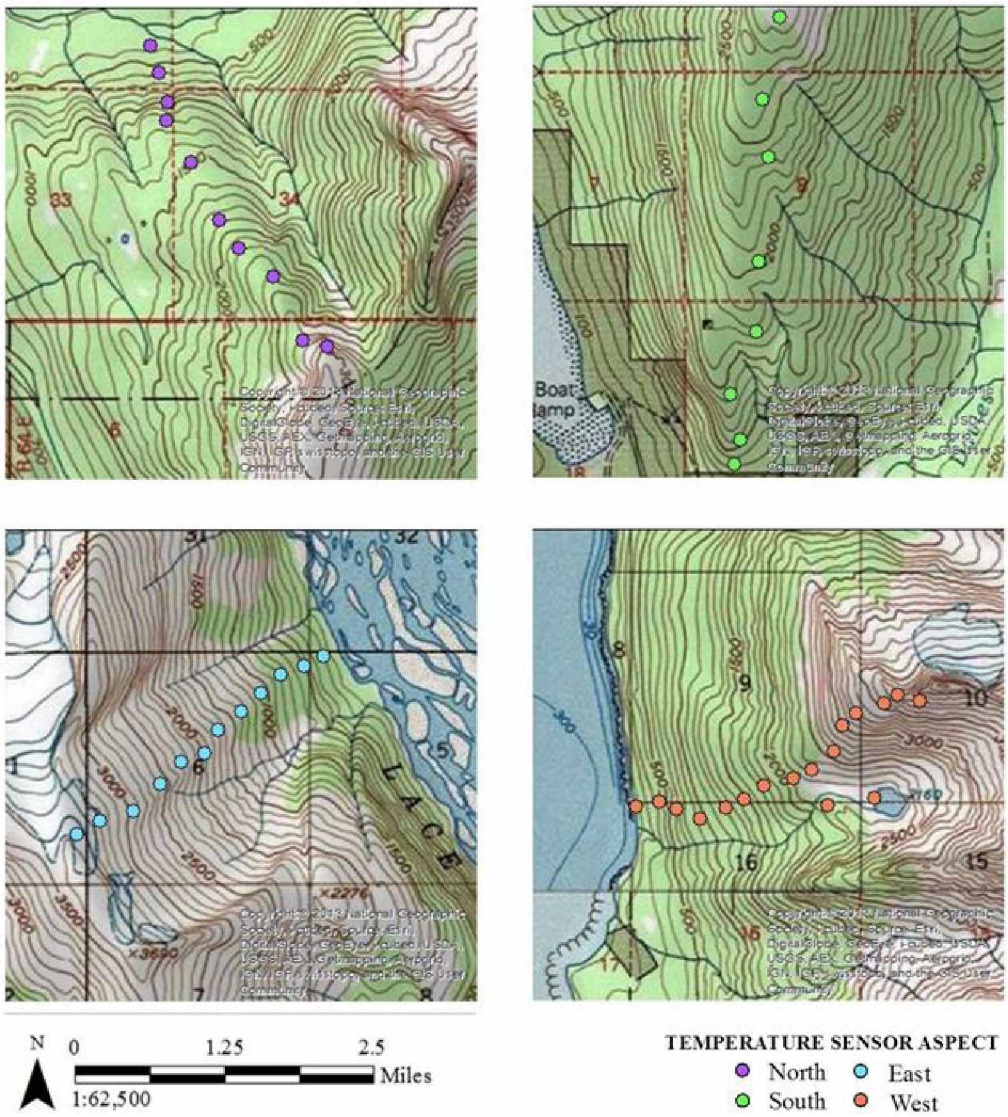

Figure 4. Contour map of temperature sensor transects in Berners Bay, Alaska. Locations of HOBO temperature loggers within the north transect (top left) are shown with purple circles. Locations of HOBO temperature loggers within the south transect (top right) are shown with green circles. Locations of HOBO temperature loggers within the east transect (bottom left) are shown with blue circles. Locations of HOBO temperature loggers within the west transect are shown with brown circles. Topographic contours on the map indicate changes in elevation.

Every effort was made to eliminate the potential for biased readings by the thermistors from direct exposure to both solar radiation and external meteorological influence. To prevent erroneous temperature measurement due to direct and reflected solar radiation, I used Gill-style solar radiation shielding for each logger (Holden et al., 2011; Hubbart, 2011; Hubbart et al., 2005; Huwald et al., 2009; Lin et al., 2001; Lundquist and Huggett, 2008; Marshall et al., 2007; Tarara and Hoheisel, 2007; Whiteman et al., 2000). Below the tree line, housed sensors were hung in trees in an effort to further reduce the occurrence of biased readings due to solar exposure (Figure 5).

Figure 5. Sensors deployed within solar radiation shield. Sensors pictured were deployed above (A), and below (B) tree line in Berners Bay. HOBO temperature loggers were suspended within the internal column of the Gill-style radiation shield. Plates above and below the cones blocked reflected light from entering the column. Photos: Jeffrey Frederick.

Lundquist and Huggett (2008) demonstrated that this method for sensor deployment was effective at reducing the risk of solar radiation influencing readings of air temperatures by HOBO data loggers. Sensors were tied to, or hung from trees at a height not to exceed 2m in an effort to capture the near-surface air temperature. Above tree line, sensor housings were attached to large boulders or rock outcroppings with rope (Figure 5). When choosing locations for sensor deployment, sites for each transect were also subjected to the criterion that, if possible, transects would be deployed on a ridgeline. Deployment of sensors on ridgelines was conducted in an effort to mitigate biased readings due to the effects of channeled airflow, inversions, and cold air pooling. These meteorological phenomena are common to mountainous regions where mountain bowls and/or valleys are present.

I deployed four transects (46 shielded sensors) that satisfied the selection criteria. The north facing transect was deployed on a ridge at the southern end of the study area and had an elevational apex of 914m. The south facing transect was also deployed at the southern end of the study area and had an elevational apex of 914m. The west facing transect was deployed on a ridgeline at the north/south "midpoint" of the bay, and had an elevational apex of 1189m. The east facing transect was deployed at the northern end of the bay, with an elevational apex of 1097m. Though the east transect was technically on a mountain slope, I selected this site as appropriate due to the lack of east-facing ridges within the study area. Nevertheless, selection of the particular slope for deployment of the east transect was done under the assumption that the sensors therein would not be strongly influenced by the aforementioned thermal/meteorological phenomena (e.g., air pooling and inversions). All loggers were deployed in the study area between June and September of 2013 and collected temperature data every hour for between 13 and 15 months continuously. The array of temperature sensors within the study area is depicted in Figure 6.

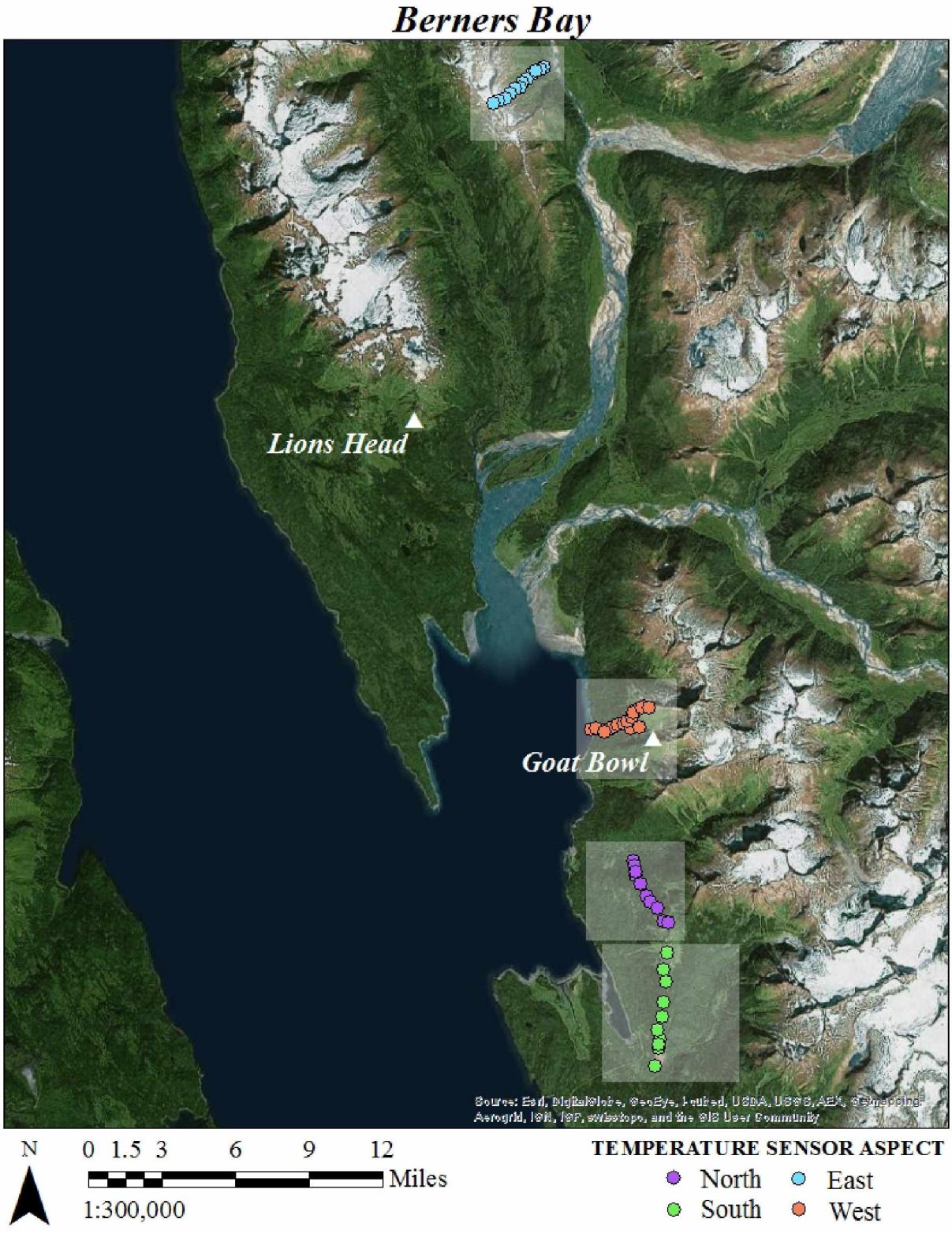

Figure 6. Spatial map of ecological sampling within the study area, Berners Bay. The temperature sensor array is highlighted with grey squares. Circles indicate locations of temperature sensors and are color coded for each of four transects, as indicated by the legend. Upward-facing triangles indicate mountain goat behavioral observation sites.

5.1.3 – Data retrieval

The data from the north and east transects respectively were retrieved on September 24, 2014. Data from the west transect were retrieved on September 26, 2014, and data from the south transect were retrieved on September 30, 2014. Of the 46 sensors deployed, 41 were recovered. As several housings and associated sensors were found dislodged from the trees within which they were hung, thermal profiles of the data were visually inspected within HOBOware Pro for erroneous readings (e.g., temperature spikes above 32°C, erratic readings of a temperature increase of over 11°C from one hour to the next). Numeric temperature readings were compiled in Excel (Microsoft Office 2010, Microsoft Corp.) and erroneous readings as determined from visual inspections in HOBOware Pro were deleted from the associated dataset and not included in the subsequent analysis. Further, thermal profiles given by HOBOware Pro for several sensors revealed they were buried by snow for several months during the winter. This occurrence was revealed by a 0°C "flatline" of the readings taken by an individual sensor during certain winter months. Data with this description were deleted from the overall dataset and not used in the following analysis. Subsequent to the quality assurance/quality control process, temperature data were analyzed to calculate lapse rates using R Statistical Software (R Core Team, 2014).

5.1.4 – Derivation of T_{avg} Near-Surface Lapse Rates

Lapse rates are defined by the decrease in air temperature due to increases in elevation. Most commonly, lapse rates are reported in terms of kilometer or hundred-meter increases in elevation whereby the value of the lapse is equal to °C $100m^{-1}$ or °C km^{-1}. The majority of published studies on lapse rates calculate the value using a simple least squares regression model (SLR) (Blandford et al., 2008; Bolstad et al., 1998; Dobrowski et al., 2009; Dodson and Marks, 1997; Gardner et al., 2009; Harlow et al., 2004; Kattel et al., 2013; Marshall et al., 2007; Minder et al., 2010; Pepin et al., 1999; Rolland, 2003; Tang and Fang, 2006). The following represents the formula for derivation of temporally averaged lapse rates:

$$T_{avg,s}=\beta X_s+t_0+\varepsilon \qquad (1)$$

Whereby, $T_{avg,s}$ is the average daily air temperature at sensor s, β is the regression coefficient for slope (lapse rate) calculated in (°C m^{-1}), X is the elevation (m) at sensor s, t_0 is the temperature (°C) at sea level, and ε is the error term. I employed this model to calculate daily T_{avg} lapse rates and illuminate the daily variability inherent to complex terrain within the northern coastal temperate rainforest. To produce average lapse rates for whole months (which generally offers more utility for modeling, hydrological, and ecological investigations), I derived T_{avg} lapse rates using a series of linear mixed effects models (LMM). I chose LMM due to the following: study design including repeated measures by an array of sensors placed at 100m intervals from sea level to site apex, the relegation of transects to represent north, south, east, and west-facing aspects, to maximize the precision for downscaling applications, and to better

generate longitudinal history of lapse rate variability. As the nature of the data encompasses aspects of both repeated-measures pseudoreplication and time-series longitudinal measure, linear mixed effects models allow a temporal block (i.e., a month) to be treated as the sample space with average daily temperatures reported by each sensor acting as "locations" within that space. The addition of random effects within the lapse-rate analysis thus accounts for the variance-covariance structure of the fixed effects (mean temperature and elevation) with regard to selected random effects, thus mitigating the ability of outliers or days with temperature extremes to skew the underlying fundamental relationship between temperature and elevation (Crawley, 2012) as well as addressing the non-independent spatial correlation and pseudoreplication between "neighboring" sensors. The following represents the linear mixed effects model used in this study:

$$T_{avg,s}=\beta X_s+\gamma Z+t_0+\varepsilon \qquad (2)$$

whereby $T_{avg,s}$ is the average daily air temperature at sensor s, β is the model coefficient for slope (lapse rate) calculated in (°C m^{-1}), X is the elevation (m) at sensor s, γ is the vector of j random effects concomitant to Z, Z is the $n \cdot j$ model matrix, t_0 is the temperature (°C) at sea level, and ε is the error term. For both models, hourly temperatures taken by each sensor in a given day were averaged (arithmetic mean) to calculate a daily average temperature. Successive SLR models were run for each day (n=440 sampling days) of the study period, and the β coefficient (slope) for each model was extracted to derive daily lapse rates. The coefficient of correlation (r) was also extracted to determine the strength of the temperature-elevation relationship through time.

Average daily temperatures were then manually partitioned into monthly block datasets. Linear mixed effects models were run in R using the Lme4 package (Bates et al., 2015). Mixed effects models were fit to the data with restricted maximum likelihood estimation (REML) using combinations of random effects to include aspect/transect, sensor, and date. The aspect-based random factor accounts for random variation in transect- or mountain-specific temperature anomalies. Such anomalies could skew the true mean lapse rate for the entire study area if the random factor was not incorporated within the model. The sensor-based random factor accounts for not only accuracy or mechanical differences between sensors, but also for random variation associated with the spatial differences unique to all respective sensors. The aim to measure lapse rates across the full montane elevational gradient fundamentally requires that near-surface air temperature be measured in both open (e.g., alpine) or closed (e.g., forested) habitat types. Consequently, inherent spatial differences between sensor locations (spatial autocorrelation), micro-climate temperature anomalies unique to any one sensor, and the variation between degrees of open versus closed canopy cover under which any sensor was deployed, were important statistical considerations. The inclusion of sensor as a random factor in the mixed effects model approach appropriately accounts for these sampling design issues, whereas the majority of lapse rate

studies published in the literature (using SLR) are deficient in this respect. Moreover, the aim to measure near-surface lapse rates was fundamentally rooted in attempting to inform ecological studies of fauna near the ground surface. Biologically speaking, organisms do not experience ambient temperature at a fixed openness category. Even sessile organisms like plants will not be subject to a fixed open or closed radiation exposure type throughout their lifecycle. The objective was thus to calculate lapse rate of air temperature within 2m of the ground's surface regardless of cover type. As such, the use of sensor as a random effect accounted for the slight differences between microclimates at each sensor location. Lastly, as I aimed to explore the variances in random effects that contribute to lapse rate variability over time, REML-fit models were more appropriate than maximum likelihood models because they produce unbiased variance estimates (Crawley, 2012; Faraway, 2005).

I determined the best-fit model using Q-Q plots for normality, maximum likelihood ratio tests (MLRT), and residual analysis of random effects (including residual v. fitted values and residuals v. response plots). The MLRT served to assess the probability of the collected average temperature observations given the respective model. As the MLRT requires a mixed effects model to be fit via maximum likelihood (ML), rather than REML, the models were re-run under this criterion to perform the tests (Bolker et al., 2009; Crawley, 2012; Faraway, 2005; Pinheiro and Bates, 2000). Overall, the MLRT allows for the comparison of two models: the first being a full model to include the factor of interest, and the second acting as a null model without the factor of interest. Models were fit stepwise, firstly including all random effects (Peterson and Ver Hoef, 2010). All random effects combinations were then sequentially compared to null models with the factor of interest removed using the MLRT for each combination. An additional maximum likelihood ratio test was then performed to test the validity of the temperature/elevation relationship. A null model was constructed from the pre-determined best-fit model by removing elevation as a fixed effect, and diagnostic measures including AIC, BIC, and P-values from chi-square tests were investigated to determine the significance of the best fit model in comparison to the null. The 95% confidence interval for each monthly lapse rate model was calculated in R. Following the derivation of mean lapse rates for each month during the study period (15 months), monthly lapse rates were averaged to create seasonal lapse rates, as well as an annual lapse rate for the region.

To explain the variability attributed to the temperature-elevation relationship for near-surface lapse rates, I conducted variance component analysis (Crawley, 2012) on the mixed effects models for monthly time blocks. A secondary benefit to this analysis was a confirmation of model fit appropriateness, as consistently low variance values attributed to a random effect warrants exclusion of that factor from the model. The percent variation within the best-fit model (under REML criterion) attributed to each random effect was calculated from summary output in R. Variation estimates for the model including the random effects and the residual (error) term were first summed to calculate the total

random effect variance (Crawley, 2012, Faraway, 2005; Peterson and Ver Hoef, 2010). Each individual variance value was then divided by the total variance and multiplied by 100 to attain the proportion of the model variance owed to each random effect (i.e., quantifying it's "worth") (Crawley, 2012; Peterson and Ver Hoef, 2010).

Data were then subsequently demarcated by transect to investigate aspect-level differences for mean monthly and seasonal near-surface lapse rates. The pre-determined best fit linear mixed effects model that included daily mean temperature and elevation as fixed effects, with date and sensor serving as random effects was used to calculate the aspect-level lapses. Monthly aspect-level lapse rates were then grouped and averaged according to season. Two versions of annual means were calculated for the overall lapse rate averaged across all months sampled, as well as an annual mean for which inversion months were removed from the dataset. Although both are studied here, the non-inversion month annual mean is more representative of biologically productive periods of autumn, spring, and summer.

5.2 – Mountain Goat Behavioral Monitoring

5.2.1 – Behavioral Observations

The behavior of mountain goats was characterized using both continuous focal animal sampling and instantaneous scan sampling (Altmann, 1974; Bart et al., 1998; Dawkins, 2007; Martin and Bateson, 1993). Observations were conducted during June through September (2013 and 2014). Animals were not handled or sampled in any way other than non-invasive visual behavior recording, and as such, field work was approved under an observational IACUC protocol, administered by the University of Alaska Fairbanks (UAF IACUC project: 464644-1). Mountain goats were not sampled within two hours of arrival at a field site and no instances of mountain goats fleeing as a result of our arrival occurred. Field investigators viewed mountain goats at a distance of between 800 – 2000m from a location that was isolated from the animals so as to reduce chances that our presence affected mountain goat behavior. Mountain goats were observed using tripod-mounted high-powered spotting scopes with 20-60X magnification (Barska Blackhawk Angled Spotter – Model AD11284, Barska Corp. – Pomona, CA). As a result of the often inclement weather in Southeast Alaska, mountain goat behavioral observations were opportunistic – taking place whenever viewing was possible between 06:00hr and 22:00hr. Field stints generally lasted for 8 or 9 days at a time. Data resulting from observations were only used if: (a) mountain goats were viewable for at least one hour, (b) periods of the animal moving out of sight (OOS) was less than 50% of the sampling period, and (c) in surveys that contained OOS periods, investigators were positive (based on unique physical characteristics) that the mountain goat(s) they observed were the same animal(s) being sampled prior to any period(s) of visual obstruction. Otherwise, surveys were aborted

and/or the resulting behavioral data were not used for the analysis. The 1-hour threshold for minimum observation time was conservative compared to methodologically similar behavioral studies (Amato et al., 2013; Aublet et al., 2009; Hamel and Côté, 2008; Rachlow and Bowyer; 1994). Both male and female adult mountain goats were observed for this study, whereas young/yearlings were not due to the high degree of behavioral non-independence with their associated female. Prior to the start of a survey, mountain goats of interest were subject to a few minutes of preliminary observation/viewing in order to determine the sex of the animal. Sex was easily distinguished by observing horn structure, the presence viewable genitalia (in males), defecation posture (which differs markedly between males and females), and group size/composition.

The behavior of mountain goats was characterized as follows: feeding, bedded, walking, running, standing, grooming, vigilance, and social interaction. Simultaneous behavior was not "allowed" insofar as animals in a standing posture while actively feeding were considered feeding. Likewise, animals grooming while standing or bedded were considered grooming, animals actively feeding and taking three or less steps were feeding and not considered walking, and animals engaged in vigilance were not recorded as standing or bedded during that bout. Vigilance constituted sudden changes in the direction or posture of the head (while standing or bedded), and was generally easily distinguished from other behaviors because the animals could be observed scanning the landscape, looking directly at a potential threat, or interrupting another behavior suddenly to investigate a sight or sound. Standing constituted a head forward - eyes forward posture, and generally coincided with periods of chewing and regurgitating food.

5.2.2 – Scan Sampling of Adult Mountain Goats

To investigate the proportion of behavioral states exhibited by mountain goats and the effect of various indicator variables on the activity budgets of mountain goats, I conducted instantaneous scan sampling surveys (Altmann, 1974; Bart et al., 1998; Dawkins, 2007; Martin and Bateson, 1993). When possible, scan surveys were conducted for all viewable animals on the landscape (not including individuals that were being focally sampled – description below). Prior to the start of the survey, individuals were designated with a unique ID and information on notable markings was recorded by the observer. The sex of each animal was also recorded prior to the start of the survey, as were the date, time, and local weather conditions. Scans were initiated by recording the instantaneous behavior of viewable animals from left to right on the landscape. The behavior of individuals was always recorded per-goat, meaning that even if a subject changed its orientation on the landscape with respect to other animals, its instantaneous behavior at the time of the scan was still recorded for that specific animal. Scan surveys generally lasted at least one hour and the scan interval for instantaneous recording was 10 minutes (Côté

et al., 1997; Hamel and Côté, 2008). Individual scans rarely lasted more than two to three minutes and 99% of scan surveys were conducted by the same individual (J. Frederick). In addition to recording behavior, at the moment of each scan covariates per individual were also recorded including: sun vs. shade, habitat type, and distance to escape terrain. Elevation was also estimated for each animal by referencing a USGS topographic map of the study site. The sun vs. shade covariate corresponded to whether or not the animal was occupying an area where it was exposed to direct sunlight. The criteria for determining these covariates were simply based on both cloud cover, and whether the animal cast a shadow. Habitat types included: snow, deciduous shrub thicket, sub-shrub (less dense and sporadically spaced shrubs), forest and krummholz, sedge/forb meadow, and rock (rocky with sparse vegetation). Talus fields, exposed bedrock areas, and cliffs were all considered rock habitat types. Distance to escape terrain was defined as distance to the nearest cliff in goat lengths and a goat length was defined as 1.5m. Each instance in which an animal moved out of view or became obstructed was recorded as out of site (OOS). Every effort was made to survey animals evenly over the course of a day and during all weather conditions that permitted viewing. Neither male nor female goats were preferentially selected as scan survey subjects.

5.2.3 – Focal Sampling of Adult Mountain Goats

To investigate the proportion of time spent on mountain goat behaviors and effect of various indicator variables on activity budgets, I conducted continuous focal animal sampling surveys (Altmann, 1974; Bart et al., 1998; Dawkins, 2007; Martin and Bateson, 1993). Individuals were selected for focal sampling by scanning all goats viewable on the landscape with binoculars and consecutively numbering each from left to right. A random number table was subsequently used to select an animal for observation. Once an animal was selected, field investigators omitted that animal from any potential scan sampling survey that may have been simultaneously occurring. As many goats were generally present on the landscape, every effort was made to ensure individuals that were focally sampled were omitted from subsequent focal samples occurring on the same day. Focal surveys generally lasted at least one hour. At the start of a focal survey, field investigators recorded the date and time, the elevation of the animal, and local weather conditions. Continuous recording was implemented, in that time and a starting behavior was recorded at the beginning of a survey, and behaviors were recorded (with a time stamp) each time a new behavior was exhibited. Time stamps were recorded to include hours, minutes, and seconds. Additionally, covariates including habitat type, distance to escape terrain, group size, and sun vs. shade (all described above) were recorded at the start of each survey, and subsequently as any of the conditions changed. Each instance in which an animal moved out of view or became obstructed was recorded as out of site (OOS) and was considered time out. Every effort was made to survey animals evenly over the course of a day

and during all weather conditions that permitted viewing (e.g., Fox, 1978). Neither male nor female goats were preferentially selected for focal sampling and selection of focal individuals using a random number table further assisted in this effort for non-biased recording.

5.2.4 – Reference Goat Elevation Sampling

In order to investigate linkages between mountain goat elevation, temperature, and behavior, I obtained datasets from two radio-collared mountain goats within the study area. These data were collected under the auspices of research conducted by the Alaska Department of Fish and Game. The goats' collars contained an internal thermistor, and activity sensor, and a mortality sensor. Both mountain goats inhabited the same sites as were used for behavioral observation. Collar data used in the analysis did not include years wherein behavioral observation took place. For each animal, I analyzed data on date, time, temperature (°C), and elevation. The use of these data was a valuable tool with which I could potentially corroborate any findings from the focal and scan surveys pertaining to goat elevation and temperature relationships. The first collared individual was a 7-year-old male when originally captured in 2010, and the second individual was a 4-year-old female when originally captured in 2008. The dataset used as reference for this study was reduced by only analyzing data for summer/autumn months, so as to match the time of the year when I sampled behavior (i.e., June – September). Though a sample size of two collared mountain goats lacks statistical power, these data served to support or contradict any temperature-elevation relationship explained by the focal and scan data sets. As scan and focal samples were collected across unidentified individuals and a wide temporal extent, the use of fine-scale data on collared individuals within our study area were a valuable comparative tool. Illuminating whether or not any relationships revealed by scan and focal data sets were chance artifacts of sampling design aided in making this analysis more robust. Should a relationship between temperature and mountain goat elevation be explained by the scan and focal samples, the signal should thus be present within the collar data. To this end, I intended to validate my observational findings by comparing them to radio-tracked individuals within our study area, controlling for autocorrelation by using data for different years (than I sampled behavior), as well as using an independent method of temperature measurement (i.e., the within-collar thermistor rather than the sensor array).

5.2.5 – Statistical Analyses

Activity budgets were created from focal and scan data sets following Hamel and Côté (2008) and Du Toit and Yetman (2005). For focally sampled animals, the hourly proportion of time spent engaged in each behavior was calculated, and taken together constituted an individual's activity budget.

For scan-sampled groups, the proportion of occurrences of a respective behavior state taken across all scan intervals for all individuals within the group constituted the hourly activity budget.

The resulting proportions/percentages were arcsine-square root (angular) transformed to ensure the data met the assumption of normality. The presence of many values of 0 (behavior not recorded) and/or 1 (behavior recorded as 100% of the survey/time) indicated the need for angular transformation. By nature, angular transformations are mathematically tenuous when the frequency of 0 and 1 values proliferate because the transformation itself is based on radians (multiplication of π). As such, 0% or 100% behavioral proportions within the raw data were themselves transformed to reflect (1/4n) instead of 0, and (1 - (1/4n)) instead of 1, prior to arcsine-square root transformation (Kasuya, 2004).

I performed principal components analysis (PCA) on the transformed data for both focal and scan datasets. All statistical analyses were conducted using R statistical software (R Core Team, 2014). PCAs were performed using the correlation matrix of transformed behavioral activity budget data for both sampling methods. Angular transformation and PCA induced normality and independence between (and among) behavioral categories, but also mitigated levels of pseudoreplication inherent to this type of data (e.g., behavioral non-independence, repeated measures, and longitudinal data). A critical benefit of PCA within a behavioral framework is that orthogonal transformations render the resultant eigenvectors (behavioral principal components) independent from one another, and in addition, the PCA scores produced are linearly independent representations of a whole budget. Investigation of the PCA loadings also aid in ease of interpretation, enabling the investigator to observe which behaviors within the budget trend together, which are opposed, and which behaviors within the budget contribute to the majority of variation. Furthermore, the opposition relationship between eigenvectors can be interpreted statistically as trade-offs (e.g., Côté et al., 1997; Hamel and Côté, 2007) – the identification of which were of crucial importance to this study.

I used the PCA scores for each dataset in linear mixed effects models to test the influence of several indicator variables on the mountain goat activity budgets. In each case, the scores of each eigenvector served as the response variable. Indicator variables of interest were temperature (˚C) at the time of survey (T˚), maximum daily temperature (˚C) per survey date (T˚M), period of day divided into morning, midday, and evening (POD1), period of day divided into midday and pooled morning and evening hours (POD2), sex of the animal (for pooled scan and focal sets), and finally whether the survey took place on a warm (> 15˚C) or cool day (< 15˚C) (WC). I selected ±15˚C as the demarcation between warm days and cool days based on the upper critical threshold air temperature reported for moose (14˚C) and alpine ibex (15˚C) (Aublet et al., 2009; Renecker and Hudson, 1986; Schwab and Pitt, 1991; Van Beest and Milner; 2013; Van Beest et al., 2012). As ibex are an ecologically similar species to mountain goats in niche and behavioral phenotype, I considered 15˚C as a more probable ambient temperature

threshold than that of moose. Random effects for focal data included survey length, Julian date, and elevation. Random effects for scan data included group size, Julian date, and elevation. LMM fit was assessed via a stepwise method. I first used a saturated model under a Restricted Maximum Likelihood (REML) criterion and included all indicator variables. Subsequent models were fitted to include all combinations of indicator variables (including models with only a single indicator). Models were checked for random effects homoscedasticity, normality, and linearity by visually assessing Q-Q normality plots, residual versus fitted value plots, and response versus fitted value plots. I used maximum likelihood ratio tests (MLRT) on non-REML fit versions of each model to compare the separate models containing different combinations of indicators and determine the best fit. Best fit from the MLRT was assessed via AIC scores and chi-square (X^2) tests. Only models that were significant ($\alpha \leq 0.05$) in favor of rejecting the null were reported herein.

Following LMM analysis of mountain goat activity budgets, I conducted an analysis testing the effect of temperature on mountain goat elevation. I used simple correlation analysis as well as LMMs (REML fit) that included elevation as the response and temperature (°C) as the indicator. Random effects for focal samples included Julian date, survey length, and maximum daily temperature. Random effects for scan samples included Julian date, group size, and maximum daily temperature. I suspected that mountain goats may be responding to heat stress by adjusting their elevation; however, if true, maximum daily temperature may have influenced an animal's elevation prior to the start of a survey. As such, the use of maximum daily temperature as a random effect in the temperature-elevation models curbs this potential and allowed for elucidation of the "true" temperature-driven elevation response, regardless of maximum daily temperature. Models were checked for random effects homoscedasticity, normality, and linearity by visually assessing Q-Q normality plots, residual versus fitted value plots, and response versus fitted value plots. A null, intercept-only model was then constructed and tested against the LMMs using MLRTs. Best fit from the MLRT was assessed via AIC scores and X^2 tests. Lastly, I attempted to corroborate the temperature-elevation model results using collar data from the two mountain goats described in Section 2.6 (reference goat sampling). As a result of observations being conducted on non-collared animals, the extent of repeated measures could not be statistically determined. Additionally, estimation of mountain goat elevation during scan and focal surveys was conducted visually using topographic maps at the time of survey. Using data from collared animals though, allowed me to use them as a reference and confirm or deny corroboration of any relationship revealed by the LMM analysis of the observational data. The LMM analysis described above including model fit determination and significance testing against the null using MLRTs was conducted on the collared goat data using date as a random effect.

5.2.6 – Concerning Pseudoreplication

Considerations pertaining to pseudoreplication within this study included pooling fallacy, behavioral non-independence, group-level non-independence, and longitudinal repeated measures. The design of this project (in terms of ameliorating pseudoreplication) followed Côté et al. (1997) and Hamel and Côté (2008). Aublet et al. (2009) conducted a somewhat similar study on alpine ibex, yet used generalized linear mixed models to mitigate pseudoreplication. With this approach, raw proportion data are used directly with the model, which is subsequently assigned a binomial family and integrates a logit link function (a logistic regression model allowing random effects). This method is effective; however, a primary difference between the sampling design used by Aublet et al. (2009) is that all ibex within the study were equipped with radio collars and therefore animal ID could be used as a random effect to mitigate repeated measures. Through careful consideration, I have concluded that this approach was the best and most effective way to address pseudoreplication given my field restrictions. Though animals were not collared in this study, the potential for the aforementioned degrees of pseudoreplication to increase the chance of a type I error was well mitigated (if not wholly eliminated). The comprehensive statistical methods using mixed effects models in concert with principal components analysis and arcsine-normalized proportion data was robust to ameliorating statistical non-independence.

Chapter 6 – Results

6.1 – Lapse Rate Monitoring

6.1.1 – Daily Near-Surface Lapse Rates

Average temperature near-surface lapse rates calculated from least squares regression models showed a high amount of variability across daily scales. The daily variation in lapse rates demonstrates the tenuous use of a -0.6 to -0.65°C $100m^{-1}$ lapse rate for a climatically dynamic area with complex terrain at high latitudes (Figure 7).

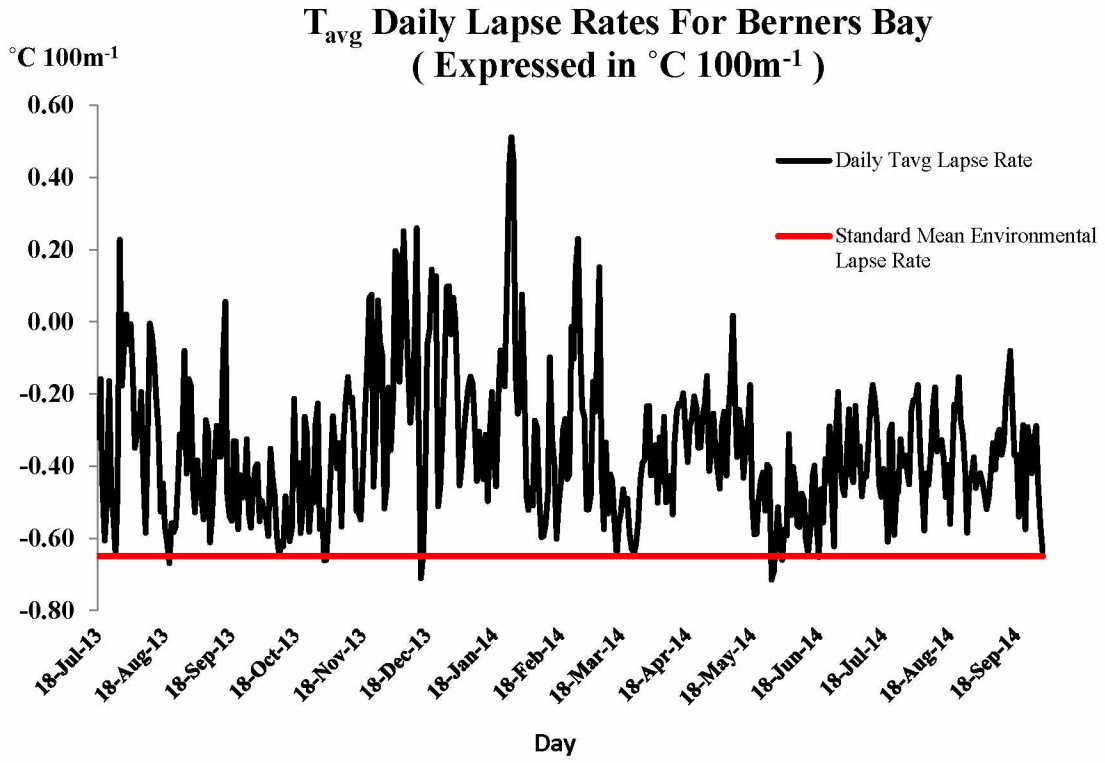

Figure 7. Time Series of Average Daily Near-Surface Temperature Lapse Rates. The time series spans the entire study period from July 2013 to September 2014. Lapse rates are expressed in °C $100m^{-1}$. Daily mean near-surface lapse rates calculated using least squares regressions are represented by the black line. The red line indicates the often cited standard mean environmental lapse rate. Temperature measurements were collected using HOBO data loggers.

Generally, daily lapse rates were less steep than the global standard and inversion-driven lapse rate reversals were measured in this study area between November 2013 and March 2014. Overall, variability

in day-to-day lapse rates was lower in the summer months and more erratic in the winter. The monthly average values of correlation coefficients (r) across the time series of the study period demonstrate seasonal variability in the linear dependence and correlation (or lack thereof) of near-surface lapse rates (Figure 8).

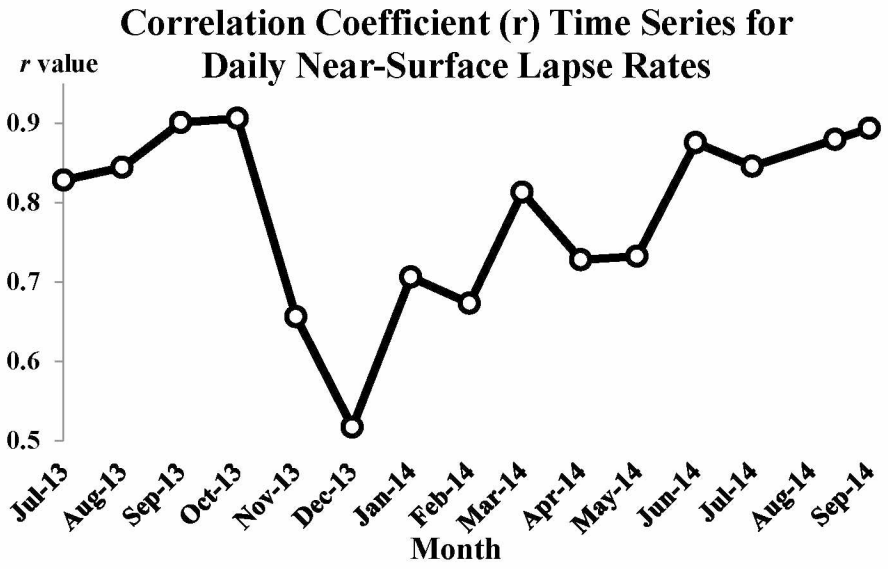

Figure 8. Time series graph of the annual variability of daily mean near-surface lapse rates. The time series spans the entire study period from July 2013 to September 2014.The correlation coefficient (r) was obtained from least squares regressions between average daily temperature (˚C) and elevation (m). Open circles indicate the mean correlation coefficient for each month. Mean temperatures were calculated using HOBO data loggers.

The temperature-elevation relationship sharply decreases in October culminating in a December nadir of least correlation. Throughout the winter, the relationship remains weak until the occurrence and influence of cold air pooling and inversions abates in spring. Interestingly, the data capture the apparent influence of synoptic weather patterns causing steep changes in air pressure, resulting in single-day inversion events even during the summer months (Figure 7). The highest inversion-driven lapse rate reversals noted during the study period occurred between January 25 and January 27 with recorded increases of temperature with elevation reaching +0.43˚C $100m^{-1}$, +0.51˚C $100m^{-1}$, and +0.45˚C $100m^{-1}$ respectively. In general, lapse rates from April through September fluctuated between roughly -0.20˚C $100m^{-1}$ and -0.58˚C $100m^{-1}$.

6.1.2 – Monthly Near-Surface Lapse Rates

Monthly T_{avg} lapse rate model validation procedures revealed the best-fit model to include mean temperature and elevation as fixed effects, while sensor and date (respectively) served as random effects. Diagnostics and residual analysis of the random effects were well behaved, exhibiting both normality and homoscedasticity. In observing the response verses fitted/predicted values from the model, the resultant tight clustering of points around the X=Y line suggested strong linearity and the effectiveness of the temperature-elevation model to predict what was measured in the field (Figure 9).

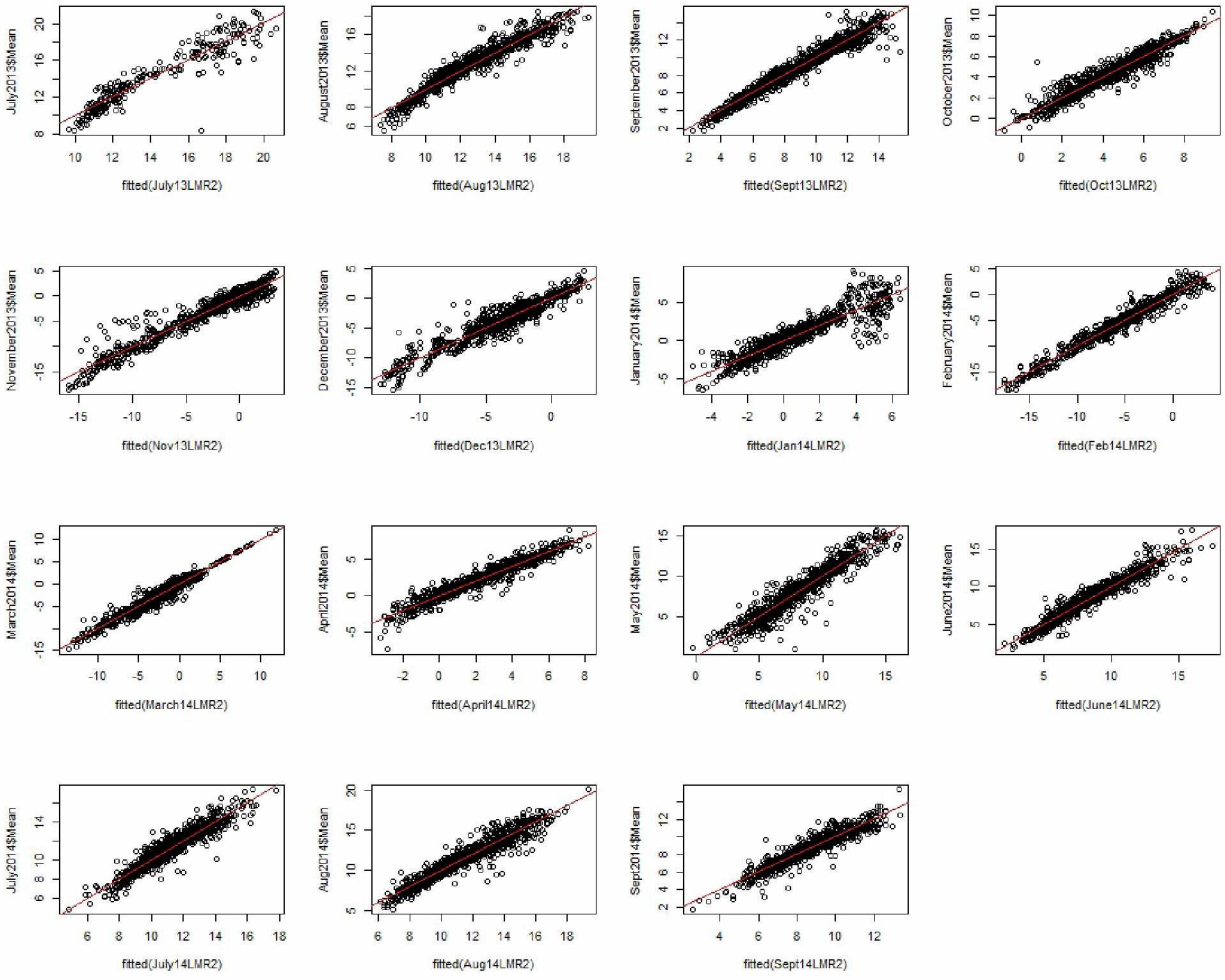

Figure 9. Plots of model response (mean temperature) versus fitted values. Monthly lapse rated were calculated using linear mixed effects models, including date and sensor as random effects. Open circles represent the nexus of mean temperatures and model fitted values. An X = Y regression line is shown in red within each plot for ease of interpretation and assessment of linearity / goodness of fit for the temperature elevation relationship. All temperature measurements were sampled using HOBO data loggers from July 2013 to September 2014 in Berners Bay, Alaska. Lapse rates were averaged across four transects, each facing one of the four cardinal directions.

Average monthly lapse rates were variable between months, yet showed a predictable trend of steeper lapses in summer and weak lapses in winter (Figure 10).

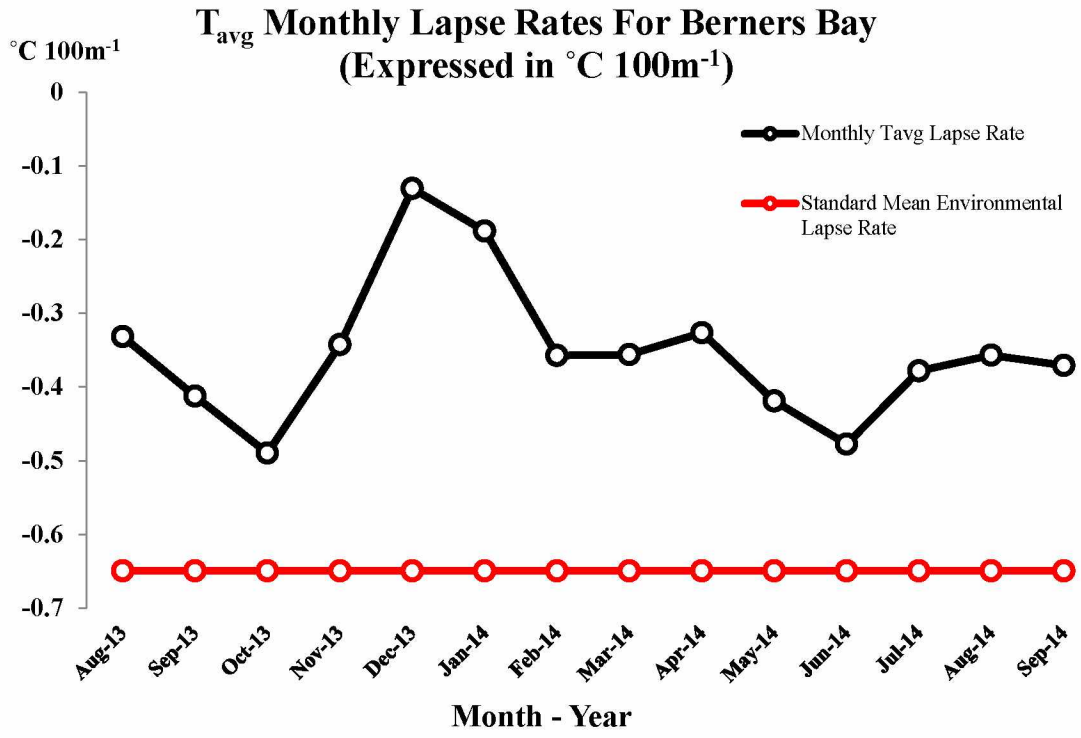

Figure 10. Time series of monthly T_{avg} near-surface lapse rates. The time series spans August 2013 to September 2014. T_{avg} lapse rates are expressed in °C 100m^{-1}. Monthly mean near-surface lapse rates were calculated using linear mixed effects models and are represented by the black line. Open black circles represent the average monthly lapse rate. The red line with open circles for each month indicates the often cited standard mean environmental lapse rate. Temperature measurements were collected using HOBO data loggers.

The steepest lapse rate during the study period was observed in June of 2014 at -0.5021°C 100m^{-1}. More generally, lapse rates for Berners Bay in summer fluctuated between ~-0.33 and ~-0.42°C 100m^{-1}. The weakest lapses for the study period were, not surprisingly, observed in winter with the December 2013 lapse rate measuring -0.0834°C 100m^{-1} and the January 2014 lapse rate measuring -0.1849°C 100m^{-1}. The time series of monthly T_{avg} lapse rates, depicts an interesting topology, in that fluctuating lapse rates in summer commence a notable, somewhat sequential increase in steepness into fall, culminating in one of the steepest lapse rates measured during the study (October 2013, -0.4961°C 100m^{-1}) (Figure 10). Subsequent to the fall lapse rate apex, lapses steadily declined, culminating in the weakest lapses experienced during the winter months. This abrupt shift in the "direction" of the lapse marks a telling

seasonal shift in both Southeast Alaska weather (e.g., onset of snowfall) and incidences of winter montane meteorological phenomena (e.g., inversions) that drive average temperature lapse rates toward reversal. The sequential increase (from December to March) in lapse rate steepness following the winter nadir is both indicative and intuitive given the onset of the seasonal shift into spring and summer. Though the study period included only 14 months of sampling, a clear increase in steepness of the lapse can be seen in the final months of survey, mirroring the previous fall increase. Near-surface lapse rates and a 95% confidence interval calculated on monthly scales using linear mixed effects models (REML fit) are given in Table 2.

Month	Lapse Rate	95% Confidence Interval for Monthly Lapse Rate	
Aug-13	-0.3305	-0.3767	-0.2842
Sep-13	-0.4150	-0.4556	-0.3744
Oct-13	-0.4961	-0.5427	-0.4495
Nov-13	-0.3029	-0.3900	-0.2157
Dec-13	-0.0834	-0.1450	-0.0196
Jan-14	-0.1849	-0.2522	-0.1178
Feb-14	-0.3309	-0.4226	-0.2391
Mar-14	-0.4347	-0.5206	-0.3487
Apr-14	-0.3297	-0.4363	-0.2546
May-14	-0.4263	-0.5531	-0.2996
Jun-14	-0.5021	-0.5746	-0.4298
Jul-14	-0.3989	-0.4597	-0.3384
Aug-14	-0.3629	-0.4143	-0.3114
Sep-14	-0.3616	-0.4048	-0.3182

Table 2. Monthly T_{avg} near-surface lapse rates for the period. The average monthly lapse rates span August 2013 to September 2014 and were calculated using linear mixed effects models. Monthly average lapse rates are the conglomerate of data from north-, south-, east-, and west-facing transects. The 95% confidence interval is given for the average lapse rate during each month. Lapse rates and the confidence intervals are expressed in $^{\circ}C\ 100m^{-1}$.

6.1.3 – Variance Component Analysis

Preliminary diagnostic model testing results (not shown here) showed the aspect factor as contributing almost nothing to the overall variation explained by the model when it was used as a random effect in concert with the date and sensor factors. Instead, the best-fit model included only date and sensor as random effects. Including sensor as a factor within the model may effectively account for the variability differences between transects as the variation between sensors inherently encompasses aspect-

level differences within the sampling array. Hereafter, I consider variation within the model attributed to sensors to include aspect / transect-level differences.

Overall, the date factor implemented as a random effect explained most of the variation attributed to the model. Variance percentages of the date factor in the monthly time series ranged from 60.87% in October 2013 to 96.34% in March of 2014 (Table 3).

Month	Variance Effect of Date	Variance Effect of Sensor	Variance Effect of Residuals	Sensor % Overall	Residuals % Overall	Date % Overall
Aug-13	5.2795	0.1328	0.5538	2.23%	9.28%	88.49%
Sep-13	6.3068	0.1499	0.4500	2.17%	6.51%	91.31%
Oct-13	0.8319	0.2105	0.3242	15.40%	23.72%	60.87%
Nov-13	20.2372	0.5963	1.5507	2.66%	6.93%	90.41%
Dec-13	10.1003	0.2642	1.3508	2.26%	11.53%	86.21%
Jan-14	5.1343	0.3059	1.2859	4.55%	19.11%	76.33%
Feb-14	19.0761	0.6233	0.9985	3.01%	4.82%	92.13%
Mar-14	37.2439	0.5497	0.8642	1.42%	2.24%	96.34%
Apr-14	4.4954	0.5746	0.5043	10.31%	9.05%	80.61%
May-14	4.7664	1.4056	0.9651	19.69%	13.52%	66.78%
Jun-14	3.8902	0.4772	0.5039	9.80%	10.34%	79.86%
Jul-14	1.7314	0.3585	0.4060	14.36%	16.27%	69.37%
Aug-14	6.7426	0.2261	0.5609	3.00%	7.45%	89.55%
Sep-14	1.9925	0.1538	0.4337	5.96%	16.81%	77.23%

Table 3. Variance component analysis of LMMs. Variance components are expressed in terms of each random effect. Subsequent percentages indicate the degree to which each random effect contributed to the overall variance of the model. Linear mixed effects model variances span August 2013 to September 2014.

These results highlight the large daily variation in lapse rates (see Figure 6) within a month-long temporal block. Differences in synoptic weather conditions, cloud cover, precipitation, wind, and solar irradiance between days greatly affects lapse rates across daily scales. This daily variation in weather conditions is thus factored in by including date as a random effect, without which, the model would be severely deficient. Consideration of date as a location within a monthly sampling space greatly improved the accuracy and precision of the lapse rate model.

The contribution of sensor variance to the model was highest in May 2014 at 19.69% and lowest in March 2014 at 1.42% (Table 3). In May 2014, high variation may be explained by the gradient of snowpack depth affecting different sensors on both elevational and aspect-level scales. For example, a

sensor near sea level, recording within a snow-free forest, would experience vastly different near-surface temperatures than a sensor at 4000ft above sea level that was recently exposed from within the heavy alpine snowpack. Further, the near surface lapse rate for May 2014 was among the steepest recorded during this study (Figure 9). The stark difference in temperature between low lying, snow-free sites in May and colder, snow-inundated sites in the high alpine may contribute to the observed result. Sun exposure differences between transects may also contribute to the amount of sensor factor-level variation within the May 2014 model. October 2013 had the second highest contribution of sensor variance for a monthly aspect model (Table 3). Transect specific differences in microclimate may have occurred due to Southeast Alaska's geographic orientation, whereby storm winds and precipitation brought in by the Alaska Current connect with south-facing slopes. Spatial aspect differences during this turbulent meteorological period may contribute to the high (comparative) variation of the sensor factor in October 2013.

6.1.4 – Maximum Likelihood Ratio Testing

I used maximum likelihood ratio tests (MLRT) to compare monthly null (intercept only) models without elevation as a fixed effect with full models including the elevation factor. This served to confirm and quantify within the respective models that: (1) the temperature-elevation relationship exists, and (2) I could assess the probability of temperature measurements (and subsequently calculated lapse rates) given the model. Furthermore, as linear mixed effects models, when run, do not involve the production of a coefficient of determination (R^2), a significance level, or a p-value for the fixed effects in the model, the test lends valuable insight into the strength of the temperature-elevation relationship during the given sampling period (Crawley et al., 2012; Faraway, 2005). The results of all MLRTs were significant in favor of rejecting the null model (without elevation as a fixed factor). Test results effectively captured compelling fluctuations in the strength of the temperature-elevation relationship. For example, in July 2014, elevation influenced average temperature (X^2=66.585, P=3.35e-16), inherently decreasing it by 0.3989˚C (0.0306 SE) per hundred meter increase, while in December 2013, elevation influenced average temperature (X^2=6.2356, P=0.0125), inherently decreasing it by only 0.0834˚C (0.0314 SE) per hundred meter increase (Table 4).

MLRT: Mean Temperature ~ Elevation + 1|Date + 1|Sensor VS. Mean Temperature ~ 1 + 1|Date + 1|Sensor				
Model	**AIC**	**BIC**	**Chi-SQ**	**P-value**
Aug-13 Null	2394.2	2413.6		
Aug-13 Full	2335	2359.1	61.274	4.97e-15
Sept-13 Null	2808	2828.3		
Sept-13 Full	2713.5	2738.9	96.483	< 2.2e-16
Oct-13 Null	2532.1	2552.7		
Oct-13 Full	2432.4	2458.1	101.68	< 2.2e-16
Nov-13 Null	3883.4	3903.4		
Nov-13 Full	3854.6	3879.6	30.811	2.84e-08
Dec-13 Null	3554.7	3574.5		
Dec-13 Full	3550.4	3575.2	6.2356	0.01252
Jan-14 Null	3309.8	3329.4		
Jan-14 Full	3290	3314.5	21.849	2.95e-06
Feb-14 Null	2932	2951.3		
Feb-14 Full	2902.7	2926.8	31.327	2.18e-08
March-14 Null	3265.4	3285.1		
March-14 Full	3221	3245.7	46.414	9.57e-12
April-14 Null	2412	2431.5		
April-14 Full	2380.5	2404.9	33.449	7.32e-09
May-14 Null	3526.8	3546.9		
May-14 Full	3498.8	3524	29.936	4.47e-08
June-14 Null	2887	2907.2		
June-14 Full	2819.2	2844.5	69.769	< 2.2e-16
July-14 Null	2723.7	2744.1		
July-14 Full	2659.1	2684.7	66.585	3.35e-16
Aug-14 Null	3556.5	3577.3		
Aug-14 Full	3488.3	3514.3	70.158	< 2.2e-16
Sept-14 Null	2306.8	2326.4		
Sept-14 Full	2228.9	2253.4	79.909	< 2.2e-16

Table 4. Results of maximum likelihood ratio test on LMMs. The MLRT tests the best fit model for elevation (indicator) and mean temperature (response) as fixed effects against a null model with elevation removed. The data set spans August 2013 to September 2013. AIC and BIC scores are reported for each likelihood ratio test. Chi-square values for each test are reported with an associated P-value to assess statistical significance.

Of note in this example, is the highly significant relationship ($\alpha < 0.001$) during a month like July 2014; and while the temperature-elevation relationship in December 2013 was significant ($\alpha=0.05$), it demonstrates that the temperature-elevation relationship was relatively weaker when compared with the model results from other months (Table 4).

6.1.5 – Seasonal and Annual Near-Surface Lapse Rates

Mean near-surface lapse rates for the study period in 2013 and 2014 were near -0.40°C $100m^{-1}$. In calculating seasonal means, I took the arithmetic mean of derived monthly lapse rates. July 2013 was excluded from the averaging process because of low sample size across days and sensors. Though (non-inversion) average monthly lapse rates showed fluctuation between -0.3029°C $100m^{-1}$ and -0.5021°C $100m^{-1}$, once months were averaged into seasonal blocks, lapse rate values only fluctuated between -0.3821°C $100m^{-1}$ and -0.4041°C $100m^{-1}$ (Table 5).

Months/Season	Mean Lapse Rate (°C $100m^{-1}$)
NI Months (Dec and Jan excluded)	**-0.3909**
Summer (May – Aug)	**-0.4041**
Autumn (Sep – Nov)	**-0.3939**
Winter (Dec –Feb)	**-0.1341**
Spring (March – April)	**-0.3821**
All Months	**-0.3542**

Table 5. Seasonal mean near-surface lapse rates. Sampling months span August 2013 to September 2014. The values reported herein are averaged from monthly near-surface lapse rates (previously reported). Lapse rates are expressed in °C $100m^{-1}$. The row labeled "NI Months" represents the annual average near-surface lapse rate for the study are averaged across all months except December and January. The row labeled "All Months" represents the average near-surface lapse rate for the entirety of the study period.

The average winter (inversion representative) lapse rate was quite weak at -0.1341°C $100m^{-1}$. Though the annual/study period lapse rate is -0.3542°C $100m^{-1}$, the effect of meteorological phenomena causing a weak relationship of a temperature lapse in winter warrants that I recommend the overall annual/study area near-surface lapse rate to be taken as -0.3909°C $100m^{-1}$ (mean for non-inversion months) if monthly values cannot be used, and that investigators not use near-surface lapse rate as a metric or inference tool for studies involving near-surface temperature in winter (Table 5).

6.1.6 – Aspect Level Near-Surface Lapse Rates

Interestingly, the data show congruence between lapse rates measured on all aspects from September 2013 until March 2014, when lapse rates estimated for the south- and east-facing transects diverged from the north- and west-facing transects until approximately July (Figure 11).

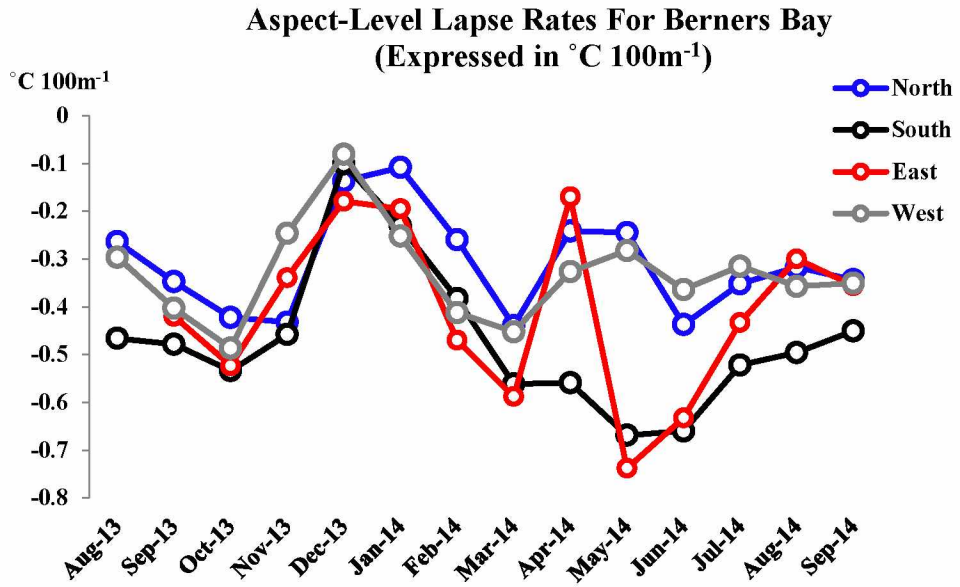

Figure 11. Time series of monthly aspect-level lapse rates. The time series spans August 2013 to September 2014. T_{avg} lapse rates are expressed in ˚C 100m^{-1}. Monthly mean near-surface lapse rates per aspect were calculated using linear mixed effects models and are represented by the blue line (north aspect), black line (south aspect), red line (east aspect), and grey line (west aspect). Open circles represent the average monthly lapse rate for the transect (aspect). Temperature measurements were collected using HOBO data loggers.

Mean monthly lapse rates on the south facing transect, unlike other aspects, continued to steepen after March, eventually reaching -0.6691˚C 100m^{-1} in May. Subsequent to this apex, the steepening trend abated and the lapse rate weakened gradually until the final measurements were taken in September 2014 (-0.4505˚C 100m^{-1}). A surprising result was that the lapse on the east-facing transect shifted erratically in this study starting in March 2014. It rapidly weakened from -0.5879˚C 100m^{-1} to a level characteristic of winter inversion months in April (-0.1703˚C 100m^{-1}), only to then abruptly reverse to the steepest lapse measured in this study during May 2014 (-0.7380˚C 100m^{-1}) (Figure 11). Although the reasoning behind this erratic variation is unclear, a combination of synoptic conditions and snow melt rates may have influenced the extreme temperature difference between low and high elevation (sensor) sites. After

inspection of the raw data (not shown here), it appeared that the sensor at the peak of the Berners-Lace ridge (1005.84 m asl) was buried under persistent snow until May 17. Sensors at the base of the ridge, however, measured mean daily temperatures between 12 and 14.8˚C (53-58.6˚F) during the first half of the month. Data during periods of snow burial for any sensor were not included in lapse rate calculation for any portion of this study. Once sensors were exposed by the melting snow pack, a combination of snow and wind affecting near-surface temperatures at high elevations, contrasted with snow-free low elevation sites (especially on sunny days), could explain the marked temperature differences responsible for such a dramatically steep lapse on the east-facing transect in May. The months May and June for the east- (-0.7380˚C $100m^{-1}$, -0.6326˚C $100m^{-1}$) and south facing (-0.6691˚C $100m^{-1}$, -0.6599˚C $100m^{-1}$) transects respectively were described by markedly steeper lapses than the temperature-elevation decreases measured at the north- (-0.2448˚C $100m^{-1}$, -0.4374˚C $100m^{-1}$) and west facing (-0.2822˚C $100m^{-1}$, -0.3640˚C $100m^{-1}$) transects, respectively (Figure 11). The strongest juxtaposition from the aforementioned example, of course, is that two transects were characterized by "winter-like" lapse rates in May, while the two others measured the steepest lapses (characteristic in summer) that occurred over the entirety of the study period. These curious results led us to search for corresponding patterns in the mean daily lapse rate dataset. Investigation of mean daily lapse rates derived from least squares regressions revealed a four-day temperature anomaly event from May 7, 2014 until May 10, 2014. During this period, mean daily lapse rates abruptly weakened to: -0.258˚C $100m^{-1}$ (R^2=0.2560), -0.164˚C $100m^{-1}$ (R^2=0.1052), 0.0171˚C $100m^{-1}$ (R^2=0.0008), and -0.207˚C $100m^{-1}$ (R^2=0.0928). The culmination of this event at full inversion above 0˚C and the correspondingly minute R^2 values confirm a complete collapse of the temperature-elevation relationship during this period. Undoubtedly, the amalgamation of anomalous synoptic weather events and stark inter-transect temperature differences resulted in incongruent lapses occurring on mountains in relatively close proximity.

Though slight for most of the study period (mean = -0.1590˚C), average monthly lapse rates within the study area showed the most notable north-south transect level comparisons in winter and spring. In November and December, when cold air pooling events and inversions were common, north-south aspect transects were most similar with lapse rates presenting as only ±0.0256˚C, and 0.0361˚C different, respectively. In late spring and early summer however, differences in the near-surface temperature lapse rates of north- and south-facing transects were ±0.3176˚C (April), 0.4243˚C (May), and 0.2225˚C (June). Overall, the results show that the mean difference in temperature shift owed to elevation alone could be ±0.38˚C $100m^{-1}$ between seasons for the same elevation.

Seasonal means of aspect-level near-surface lapse are listed in Table 4. Generally, I observed agreement between the north-west and south-east transects. Lapse rates were steeper on south and east aspects within respective seasons than their north and south aspect counterparts. For example, in summer,

north and west aspect mean lapse rates were -0.3231°C $100m^{-1}$ and -0.3230°C $100m^{-1}$, respectively, while south and west aspect mean lapse rates were -0.5626°C $100m^{-1}$ and -0.5258°C $100m^{-1}$, respectively. July 2013 mean lapse rates were left out of this analysis because of low sample size and representation of only two (of four) transects of sensors. Likewise, I could not include data from the east facing transect in August 2013 because it was the last transect deployed in September 2013. Mean annual lapse rates for the study period (not including the December and January inversion months), agreed with the overall monthly mean and annual lapse rates (e.g., pooled non-inversion annual mean = -0.3909°C $100m^{-1}$) mentioned previously (Table 2). For the north, south, east, and west aspect transects, overall non-inversion annual near-surface lapse rates were -0.3493°C $100m^{-1}$, -0.5198°C $100m^{-1}$, -0.4518°C $100m^{-1}$, and -0.3578 °C $100m^{-1}$ respectively.

6.2 – Mountain Goat Behavioral Monitoring

6.2.1 – Sampling Results

In total, scan surveys amounted to 340 goat hours with n=42 female groups surveyed, and n=18 male surveys. Focal surveys amounted to 78.6 goat hours with n=40 females surveyed, and n=29 males surveyed. The dataset from the female radio-collared mountain goat encompassed n=350 temperature/elevation measurements spanning June through August 2009. The data set for the second individual included n=366 temperature/elevation measurements spanning June through August 2011, as well as n=355 temperature/elevation measurements spanning June through August 2012. In total, the combined dataset amounted to four measurements per animal per day and an amalgamated n=1061 temperature/elevation measurements spanning 9 months and 3 (different) summers. Of all goats sampled using both methods during the study period, I observed only four instances of running behavior. As such, running behavior was removed from the subsequent analysis.

6.2.2 – Activity Budgets of Mountain Goats on Warm and Cool Days

Overall, mountain goats of both sexes spent more time foraging and bedded than engaged in other behaviors (Figure 4). Both male and female mountain goats (observed by both sampling methods) slightly shifted the proportions of behaviors within their respective budgets on warm days and cool days; however, significant shifts were not observed.

For scan-sampled animals, shifts in the hourly proportion of behavioral states exhibited were minimal with regard to standing, walking, vigilance, grooming, or social interaction behavior, whereas they were more pronounced for feeding and bedding behavior (Figure 12).

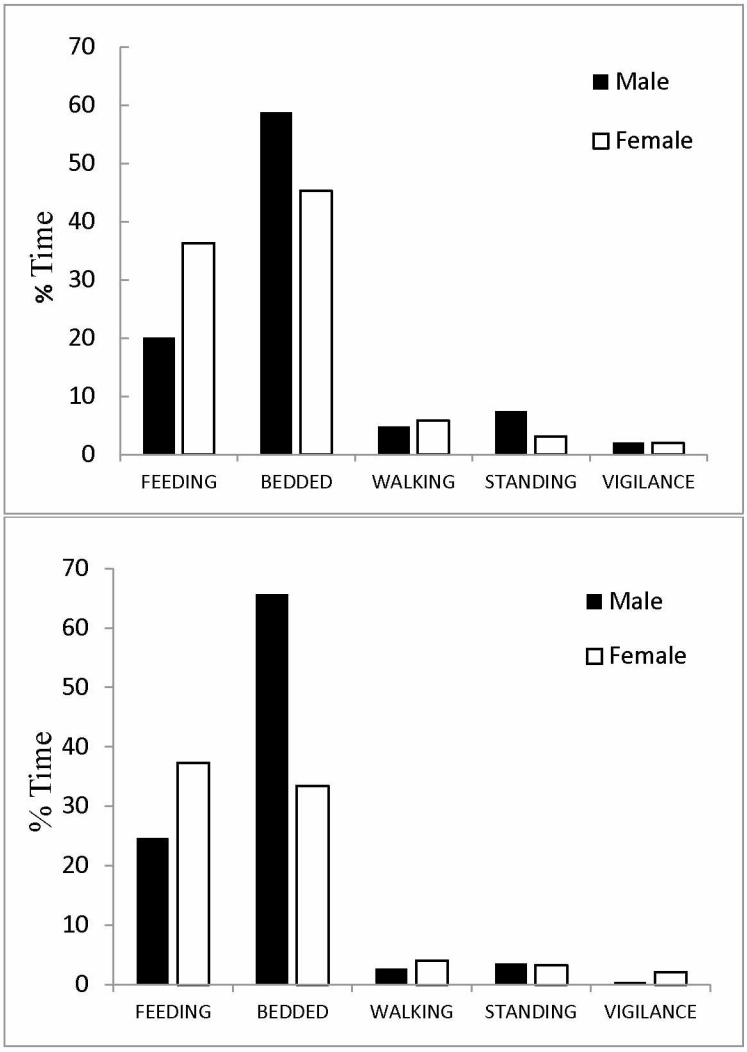

Figure 12. Warm and cool day activity budgets from focal sampling. Bar graphs pictured are for warm days (top) and cool days (bottom). Activity budgets were calculated from male and female adult goats. Survey time for focal samples total n=78.6 goat hours.

The relative differences between warm and cool day proportions of behavioral states exhibited by female mountain goats (in terms of warm days) corresponded to: a ~1% decrease of feeding behavior, a ~12% increase of bedding behavior, a ~2% increase of walking behavior, ~0.2 decrease in standing behavior, ~0.7% increase of grooming behavior, ~0.8% increase of vigilance, and a ~2% increase of social interaction with other adult goats. The relative differences between warm and cool day proportions of behavioral states exhibited by male mountain goats (in terms of warm days) corresponded to: a ~5% decrease of feeding behavior, a 7% decrease in bedding behavior, a ~4% increase in walking behavior, a ~4% increase in standing behavior, no change in the percent grooming behavior exhibited, a ~2% increase in vigilance, and no change in the percent social interaction observed.

Congruent with scan samples, mountain goats observed using focal animal sampling exhibited minimal shifts in the hourly proportion of time spent engaged in various behaviors other than feeding and bedding, with slight changes demonstrated in the amount of time spent feeding and bedding (Figure 13).

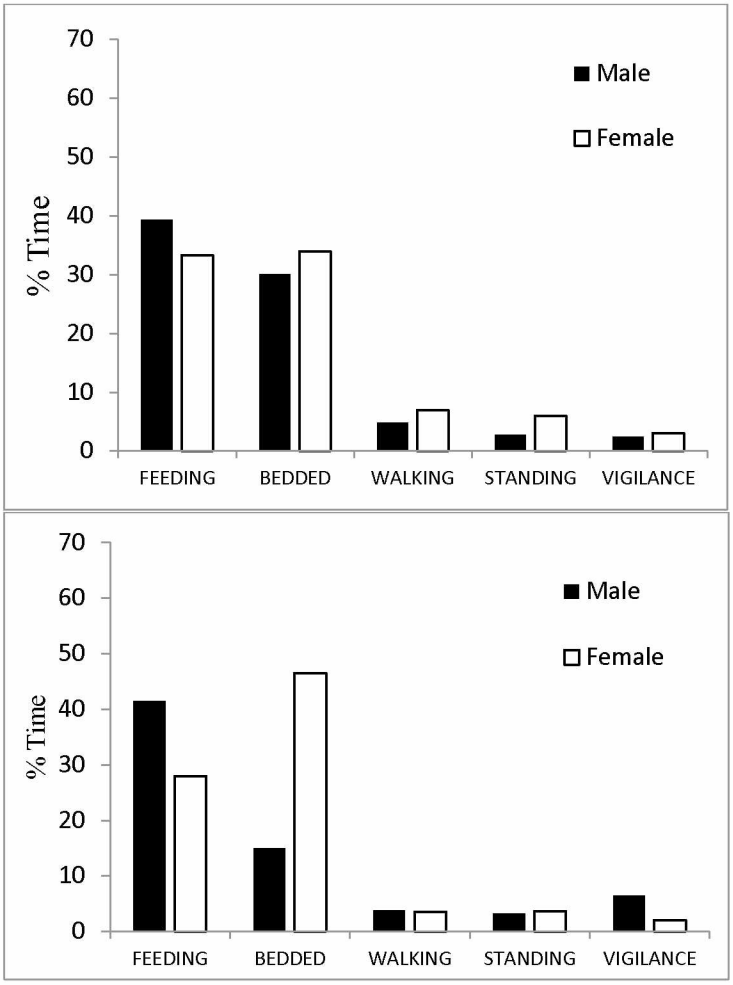

Figure 13. Warm and cool day activity budgets from scan sampling. Bar graphs pictured are for warm days (top) and cool days (bottom). Activity budgets (n = 60) were calculated from surveys of n=18 male groups and n=42 female groups of adult goats. Survey time for scan samples total n=340 goat hours.

The relative differences between warm and cool day proportions of hourly time spent engaged in respective behaviors for female mountain goats (in terms of warm days) corresponded to: a ~5% decrease in feeding behavior on warm days, a ~13% increase in bedding behavior, a ~4% increase in walking behavior, a ~2% increase in standing behavior, a ~0.25% decrease in grooming behavior, a ~1.5% increase in vigilance behavior, and a ~0.1% increase in time spent engaged in social interaction behavior with other adult goats. The relative differences between warm and cool day proportions of hourly time

spent engaged in respective behaviors by male mountain goats (in terms of warm days) corresponded to: a ~2% decrease in feeding behavior, a ~15% increase in bedding behavior, a ~1% increase of walking behavior, a ~0.5% decrease in standing behavior, a ~0.3% increase in grooming behavior, a ~4% decrease in vigilance behavior, 0.45% decrease in social interaction behavior with other adult goats.

6.2.3 – Principal Components Analysis

Results of principal components analysis for scan sampled mountain goats revealed that the first four principal components explained 80.1% of the variation in activity budgets for the combined data set, which included both sexes (Table 6).

Scan Sampled Goats (Pooled Sexes)				
Behavior	**Eigenvector 1 (32.6%)***	**Eigenvector 2 (18.3%)***	**Eigenvector 3 (16.1%)***	**Eigenvector 4 (13.1%)***
Feeding	-0.4680	-0.3480	0.4280	0.1300
Bedded	0.5770	0.1280	-0.1080	
Walking	-0.4050		-0.3950	-0.2320
Standing	-0.2100	-0.4130	-0.5260	-0.3500
Grooming	-0.2250	0.6340	-0.4400	0.1580
Vigilance	-0.4300	0.3900	0.1950	0.2740
Social Interaction		-0.3710	-0.3760	0.8400
Focally Sampled Goats (Pooled Sexes)				
Behavior	**Eigenvector 1 (32.5%)***	**Eigenvector 2 (19.7%)***	**Eigenvector 3 (16.2%)***	**Eigenvector 4 (11.7%)***
Feeding	0.4700	0.3950	0.2360	-0.3360
Bedded	-0.5660	-0.2280		0.2420
Walking	0.4540	-0.4090		0.1030
Standing	0.1860	-0.7050		
Grooming	-0.2170	-0.3200	0.5200	-0.6660
Vigilance	0.3850	-0.1500	0.2860	0.4650
Social Interaction	0.1520		-0.7640	-0.3870

Table 6. Eigenvectors calculated from principal component analysis (PCA). Principal components are derived from of adult mountain goat activity budgets. Mountain goats were observed using scan sampling (n=60 budgets) and focal animal sampling (n=69 budgets) in Berners Bay, AK (2013-2014) for a total of (n=78.6 goat hours). *Percentages attached to eigenvectors represent the proportion of overall variance in the activity budget explained by each principal component (PCA axis).

Overall, the most prominent behavioral trend as evinced by the first principal component for scan-sampled goats corresponded to the opposition of feeding and bedding behavior. The angular measures between plotted behavior categories describes that bedding behavior trended away from all others, whereas active behaviors trended together (Figure 14).

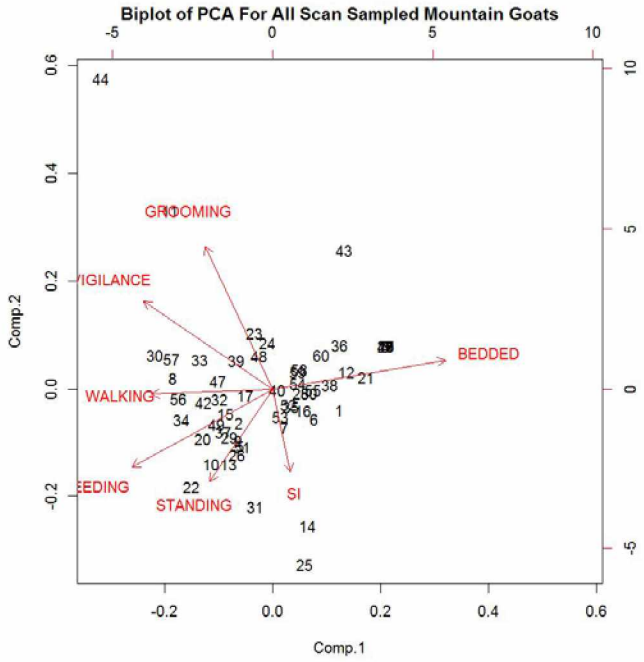

Figure 14. Biplot for scan-sampled mountain goat activity budgets. The biplot depicts the orientation of related or unrelated variables within multi-dimensional orthogonal space. The PCA is derived from n=60 scan budgets totaling n=340 goat hours.

This is a somewhat intuitive result as, for example, feeding or walking behavior may occur in concert with some degree of vigilance or standing.

Results of principal components analysis for focally-sampled mountain goats revealed that the first four principal components explained 80.1% of the variation in activity budgets (Table 6). As with scan budgets, the focal sampling PCA analysis revealed that the first principal component explaining the majority of the variation within the budget corresponded to the opposition of feeding and bedding. Focal activity budgets likewise demonstrated that active behaviors generally trended together; however, a difference between focal and scan PCAs was that grooming trended with bedding behavior in focal budgets (Figure 15).

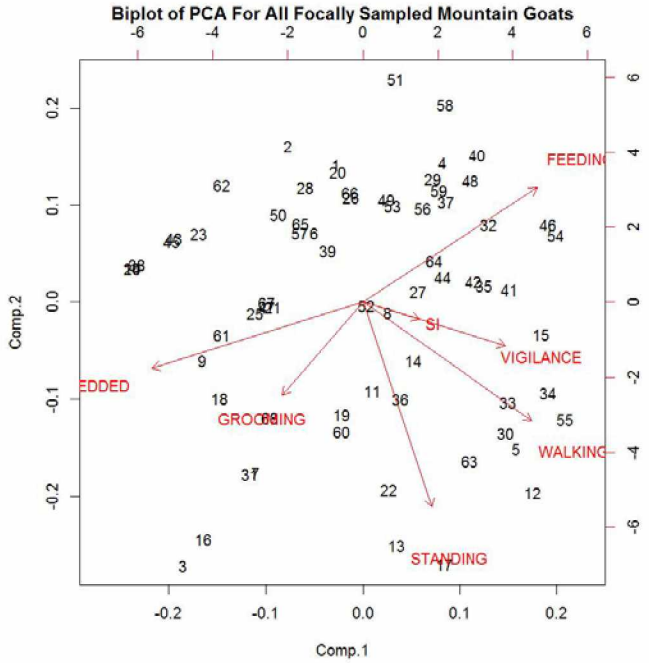

Figure 15. Biplot for focally-sampled mountain goat activity budgets. The biplot depicts the orientation of related or unrelated variables within multi-dimensional orthogonal space. The PCA is derived from focal budgets totaling n=79 goat hours.

As the first principal component explains the highest amount of variation within activity budgets (for both sampling types), PCA results demonstrate that the dichotomy between feeding and bedding is the most important aspect of overall goat behavior.

6.2.4 – Linear Mixed Effects Models on PCA Scores

Interestingly, linear mixed effects models demonstrated that temperature was not a major contributor to differences and/or variation within focal and scan samples conducted on populations of mountain goats in Berners Bay. Model results assessed via MLRTs demonstrated that both maximum daily temperature and temperature at the time of survey did not significantly affect the primary PCA axes. The major contributor to variation explained by the respective PCA axes was period of day, suggesting temporal augmentation of a baseline activity budget rather than a temperature-driven effect changing the proportions of behaviors or duration of behaviors enacted by mountain goats.

Linear mixed effects models for focal samples all included three variables used as random effects including Julian date, survey length, and elevation. The first principal component of the focal data set opposed feeding versus bedding (Table 6). The best fit model as determined by likelihood ratio tests (non-

REML fit) revealed that the indicator variables most affecting the time spent feeding versus bedding included the first period of day division (POD1 – morning, midday, evening) and sex of the animal. This best fit model demonstrated that period of day and sex decreased the second axis PCA score by -0.906 units at midday, decreased the score by -1.443 units in the morning, increased the score by 0.515 units for male mountain goats, and was significant (AIC= 254.73, X^2 = 10.064, *P*= 0.0180) when tested against the null (intercept only) model (Table 7).

Linear Mixed Models for Focally Sampled Mountain Goat Activity Budgets

FIRST PCA AXIS - Feeding vs Bedding						
Best Fit Model(s)	**AIC**	**BIC**	**Chi-Sq (P)**	**Coefficients (SE)***		**Coeff 95% CI***
I + POD1 + Sex	254.73	272.49	10.064 (0.018)	POD1 - Midday	-0.906 (0.384)	(-1.660, -0.153)
I + POD1	254.75	270.29	8.057 (0.018)	POD1 - Morning	-1.443 (0.528)	(-2.478, -0.408)
Intercept Only (null) : I	258.8	269.89		Sex - Male	0.515 (0.371)	(-0.212, 1.243)
SECOND PCA AXIS - Feeding vs Standing						
Best Fit Model(s)	**AIC**	**BIC**	**Chi-Sq (P)**	**Coefficients (SE)***		**Coeff 95% CI***
I + POD1 + Sex	214.86	232.62	9.87 (0.020)	POD1 - Midday	-0.411 (0.257)	(-0.915, 0.092)
Intercept Only (null) : I	218.73	229.83		Sex - Male	0.698 (0.273)	(0.163, 1.231)
THIRD PCA AXIS - Grooming vs Social Interaction						
Best Fit Model(s)	**AIC**	**BIC**	**Chi-Sq (P)**	**Coefficients (SE)***		**Coeff 95% CI***
n/s	n/s	n/s	n/s	n/s	n/s	n/s
FOURTH PCA AXIS - Vigilance vs Grooming						
Best Fit Model(s)	**AIC**	**BIC**	**Chi-Sq (P)**	**Coefficients (SE)***		**Coeff 95% CI***
n/s	n/s	n/s	n/s	n/s	n/s	n/s

Table 7. LMM results on focal activity budget PCA scores. LMMs tested the effect of temperature at the time of survey, maximum daily temperature, sex, period of day[1] (morning, midday, evening), period of day[2] (early and late day, midday), and warm or cool day on each of four PCA axes of adult mountain goat activity budgets derived from focal animal sampling surveys in Berners Bay, Alaska (2013—2014). Only significant models were reported. *Coefficients and 95% confidence intervals (Wald) are reported for the best fit model. N/S = no models were significant ($\alpha \leq 0.05$).

In terms of the primary behavioral opposition exhibited by mountain goats, both males and female focally sampled goats spent the highest proportion of their time feeding during either the morning or evening, while reducing their activity and comparatively increasing time spent bedded at midday. Male focal activity budgets were temporally oriented toward a higher percentage of time spent feeding in the

morning; reducing the percentage of time spent feeding at midday and in the evening by less than half the average morning value. Females demonstrated precisely the opposite, whereby time spent feeding was highest in the evening; double that of the percent time spent feeding in the morning or midday.

The second PCA axis opposed standing versus feeding. The best fit model as determined by likelihood ratio tests (non-REML fit) revealed that the indicator variables most affecting the time spent standing versus feeding also included the first period of day division (POD1) and sex of the animal. The best fit model demonstrated that period of day and sex decreased the first axis PCA score by -0.559 units at midday, decreased the score by -0.613 units in the morning, increased the score 0.803 units for male mountain goats, and was significant (AIC= 214.68, $X^2 = 9.869$, $P= 0.0197$) when tested against the null model (Table 3). In the morning, males spent double the amount of time feeding as standing, whereas during midday and evening males spent half the amount of time feeding as they did standing. Females fed most in the evening and reduced time spent feeding during midday and morning. Females stood most in the morning and decreased time spent standing by ~15% in midday and in the evening. As with the first PCA axis, the mountain goats in this study are seemed to show the exact opposite temporal orientation of their feeding vs. standing budgets according to sex: females standing most in the morning and feeding most in the evening, and males feeding most in the morning and standing most in the evening.

For the third and fourth PCA axes no models were significant over the null. This demonstrates that the variability within activity budgets attributed to time spent on these opposing behaviors for focally sampled individuals were not significantly affected by the indicator variables measured in this study.

Linear mixed effects models for scan-sampled groups all included three variables used as random effects including Julian date, group size, and elevation. The first principal component of the scan sample data set, (congruent with focal samples) opposed feeding versus bedding (Table 2). The best fit model as determined by likelihood ratio tests (non-REML fit) revealed that the indicator variables most affecting the proportions of feeding and bedding behavioral states exhibited by populations of mountain goats included the second period of day division (POD2 – morning and evening versus midday) and sex of the animal. The best fit model demonstrated that period of day and sex increased the first axis PCA score by 0.3156 units at midday, increased the score by 0.949 units for male mountain goats, and was significant (AIC= 226.5, $X^2= 6.198$, $P= 0.0451$) when tested against the null (intercept only) model (Table 8).

Linear Mixed Models for Scan Sampled Mountain Goat Activity Budgets						
FIRST PCA AXIS - Walking vs Bedding						
Best Fit Model(s)	**AIC**	**BIC**	**Chi-Sq (P)**	**Coefficients (SE)***		**Coeff 95% CI***
I + POD2 + Sex	226.5	241.16	6.198 (0.045)	POD2 - Midday	0.316 (0.381)	(-0.431, 1.063)
Intercept Only (null) : I	228.7	239.17		Sex - Male	0.949 (0.412)	(0.141, 1.757)
SECOND PCA AXIS - Standing vs Grooming						
Best Fit Model(s)	**AIC**	**BIC**	**Chi-Sq (P)**	**Coefficients (SE)***		**Coeff 95% CI***
n/s	n/s	n/s	n/s	n/s	n/s	n/s
THIRD PCA AXIS - Feeding vs Standing						
Best Fit Model(s)	**AIC**	**BIC**	**Chi-Sq (P)**	**Coefficients (SE)***		**Coeff 95% CI***
I + POD2 + WC + T°M	182.72	199.47	9.601 (0.022)	POD2 - Midday	-0.486 (0.283)	(-1.022, 0.050)
Intercept Only (null) : I	186.32	196.76		WC - Warm	-0.925 (0.583)	(-0.179, 2.028)
				T°M	-0.138 (0.054)	(-0.240, -0.356)
FOURTH PCA AXIS - Social Interaction vs Standing						
Best Fit Model(s)	**AIC**	**BIC**	**Chi-Sq (P)**	**Coefficients (SE)***		**Coeff 95% CI***
n/s	n/s	n/s	n/s	n/s	n/s	n/s

Table 8. LMM results on focal activity budget PCA scores. LMMs tested the effect of temperature at the time of survey, maximum daily temperature, sex, period of day[1] (morning, midday, evening), period of day[2] (early and late day, midday), and warm or cool day on each of four PCA axes of adult mountain goat activity budgets derived from scan sampling surveys in Berners Bay, Alaska (2013—2014). Only significant models were reported. *Coefficients and 95% confidence intervals (Wald) are reported for the best fit model. N/S = no models were significant ($\alpha \leq 0.05$).

Overall, mountain goats increased time feeding early and late in the day compared to midday, while reducing feeding behavior during midday. Bedding generally increased at midday, although this pattern was especially evident in male scan sampled mountain goats.

The third PCA axis for the scan data set opposed standing versus feeding. The best fit model as determined by likelihood ratio tests (non-REML fit) revealed that the indicator variables most affecting the proportion of behavioral states exhibited as standing versus feeding included the second period of day division (POD2), maximum daily temperature (T°M), and the distinction between a warm and cool day (> or < 15°C). The best fit model demonstrated that period of day, warm/cool, and T°M decreased the first axis PCA score by -0.486 units at midday, decreased the score by -0.138 units according to maximum daily temperature, increased the score by 0.925 on warm days, and was significant (AIC= 182.72, X^2 = 9.60, P= 0.0223) when tested against the null (intercept only) model (Table 8). Overall, females exhibited roughly the same budget on warm days and cool days in terms of feeding and standing behavior; however, males decreased the proportion of feeding behavior exhibited on warm days by ~4% and

increased the proportion of standing behavior exhibited on warm days by ~3.5% (double the cool day percentage).

For the second and fourth PCA axes, no linear mixed models were significant over the null. This demonstrates that the variability within activity budgets attributed to the proportions of behavioral states associated with these opposing behaviors for scan-sampled groups were not significantly affected by the indicator variables measured in this study.

6.2.5 – The Effect of Temperature on Mountain Goat Elevation

To assess whether goat elevation and habitat selection was affected by temperature I ran linear mixed effects models on data from two collared mountain goats within the study area (in years prior to behavioral sampling), as well as data from the scan and focal samples. Models for the focal dataset yielded no significant results when compared to the null (intercept only) model. Correlation analysis confirmed a statistically significant relation between remaining temperature and goat elevation models (Table 9; Figure 16).

Correlation Analysis Results for Temperature and Goat Elevation					
Data Set	**Pearson's *r***	***t* - Critical Value**	***P*-Value**	**95% CI**	
Scan Sampling	0.4866	4.242	8.06e-05	0.2655	0.6591
Focal Sampling	n/s	n/s	n/s	n/s	n/s
Collared Male	0.1580	4.272	2.20e-05	0.0857	0.2287
Collared Female	0.1582	2.989	0.0029	0.0543	0.2587

Table 9. Correlation analysis on temperature versus goat elevation. Pearson's product moment correlation analysis was conducted on four mountain goat data sets to assess the relation between temperature and goat elevation. Mountain goats were sampled in Berners Bay, Alaska.

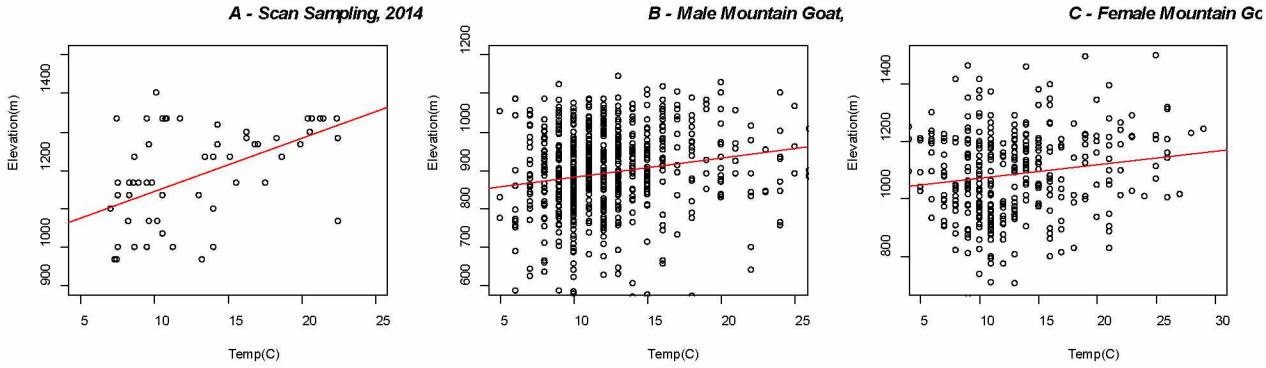

Figure 16. Regression plots for temperature versus mountain goat elevation. Data sets included scan samples as well as data from two collared mountain goats in Berners Bay, Alaska. The best-fit regression line is shown in red.

Mixed effects model analysis on the scan-sample data set revealed the best-fit model to include temperature as the only fixed effect with a quadratic function of Julian date, group size, and maximum daily temperature serving as random effects. Interestingly, the best-fit model did not include sex as a fixed effect, suggesting that the effect of temperature on goat elevation is perhaps pervasive across sexes and represents a more fundamental behavioral response to temperature for the species. Temperature affected the elevation of scan-sampled goats, increasing their elevation by 4.18m (1.09 SE) and was highly significant (AIC= 879.45, X^2 = 17.006, *P*= 2.03e-4, 95% CI= 2.045 – 6.32) compared to the null (Table 10; Figure 17).

Linear Mixed Models for Temperature and Goat Elevation						
Collared Male						
Model(s)	**AIC**	**BIC**	**Chi-Sq (P)**	**β Coefficient (SE)**		**Coeff 95% CI**
I + T°C	4335.2	4350.7	11.687 (6.294e-4)	T°C	4.76 (1.383)	(2.049, 7.471)
Intercept Only (null) : I	4344.9	4356.5				
Collared Female						
Model(s)	**AIC**	**BIC**	**Chi-Sq (P)**	**β Coefficient (SE)**		**Coeff 95% CI**
I + T°C	42404	42548	128.18 (2.2e-16)	T°C	6.10 (0.5163)	(5.091, 7.115)
Intercept Only (null) : I	42530	42428				
FOCAL SAMPLES						
Model(s)	**AIC**	**BIC**	**Chi-Sq (P)**	**β Coefficient (SE)**		**Coeff 95% CI**
n/s	n/s	n/s	n/s	n/s		n/s
SCAN SAMPLES						
Model(s)	**AIC**	**BIC**	**Chi-Sq (P)**	**β Coefficient (SE)**		**Coeff 95% CI**
I + T°C	879.45	889.92	17.006 (2.03e-4)	T°C	4.18 (1.09)	(2.045, 6.32)
Intercept Only (null) : I	892.46	898.74				

Table 10. LMM results for temperature effects on goat elevation. LMMs tested the effect of temperature at the time of survey on mountain goat elevation at the time of observation in Berners Bay, Alaska (2013—2014). Only significant models were reported. The first two table headings are reference animals that were monitored using GPS radio collars in 2009 (collared female), 2011 (from collared male), and 2012 (from collared male). *Coefficients and 95% confidence intervals (Wald) are reported for the best fit model. N/S = no models were significant ($\alpha \leq 0.05$).

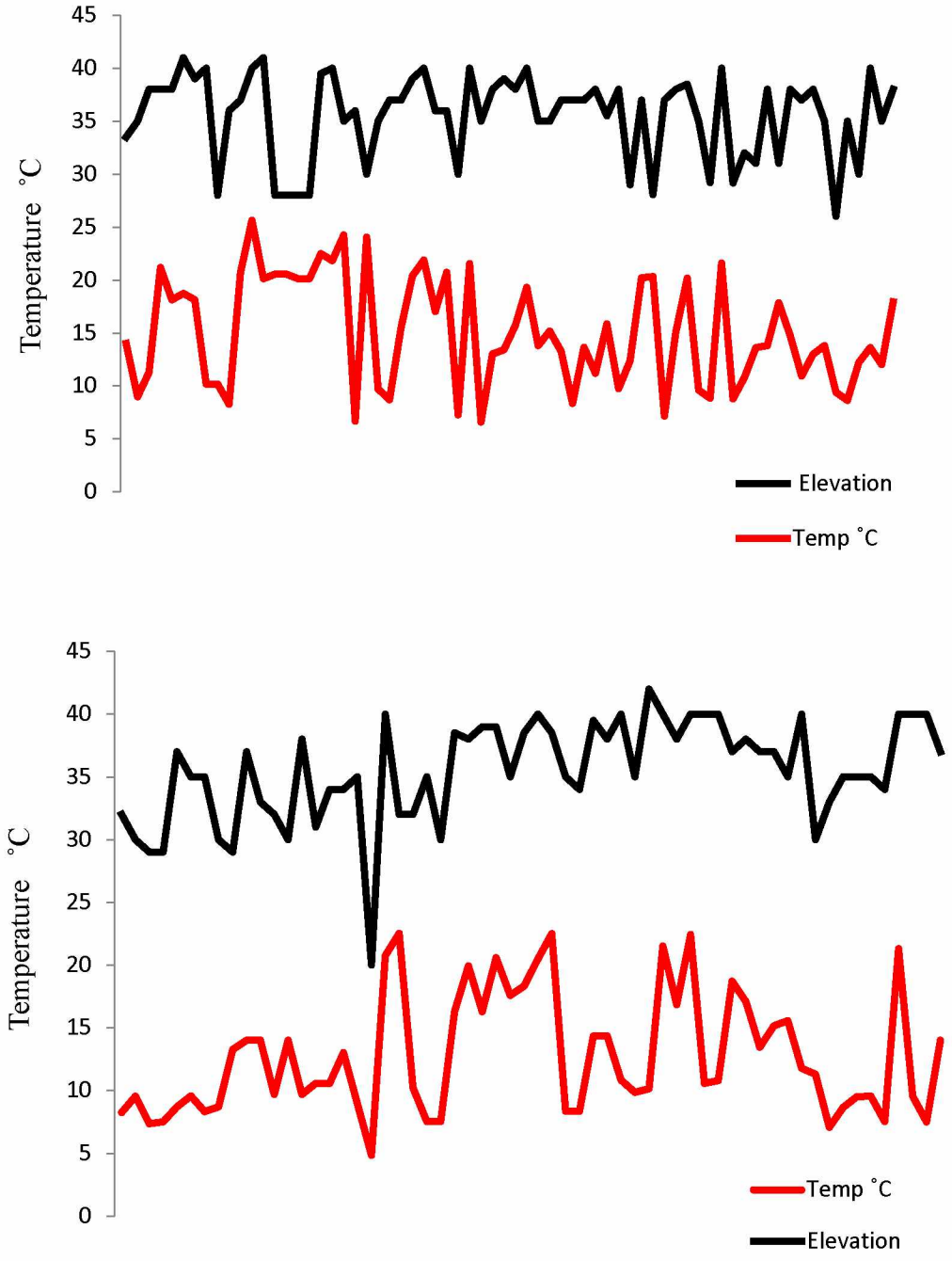

Figure 17. Stacked line graph of goat elevations and concurrent ambient temperature. Data series were taken from mountain goat behavioral surveys in Berners Bay, Alaska during summer 2013 and 2014. Behavioral surveys used focal animal sampling (top) and scan sampling (bottom) methods. Temperature data (˚C) were collected from an array of temperature loggers at observation sites stratified on the landscape in 100 meter elevational increments. Elevation data (m) were scaled for presentation purposes and are derived from visual estimations during behavioral surveys.

Although a sample size of two lacks statistical power, mixed effects model analysis on the two collared animals corroborated the findings from the scan-sampling data and demonstrated a much more robust sample size and temporal duration. The resulting best-fit model for both animals included the use of temperature and elevation as fixed effects whereas a quadratic function of Julian date served as a random effect. Temperature affected the elevation of the male collared animal, increasing its elevation by 4.76m (1.383 SE) and was highly significant (AIC= 4335.2, X^2 = 11.687, *P*= 6.294e-4, 95% CI= 2.049 to 7.471) compared to the null (Table 5; Figure 18).

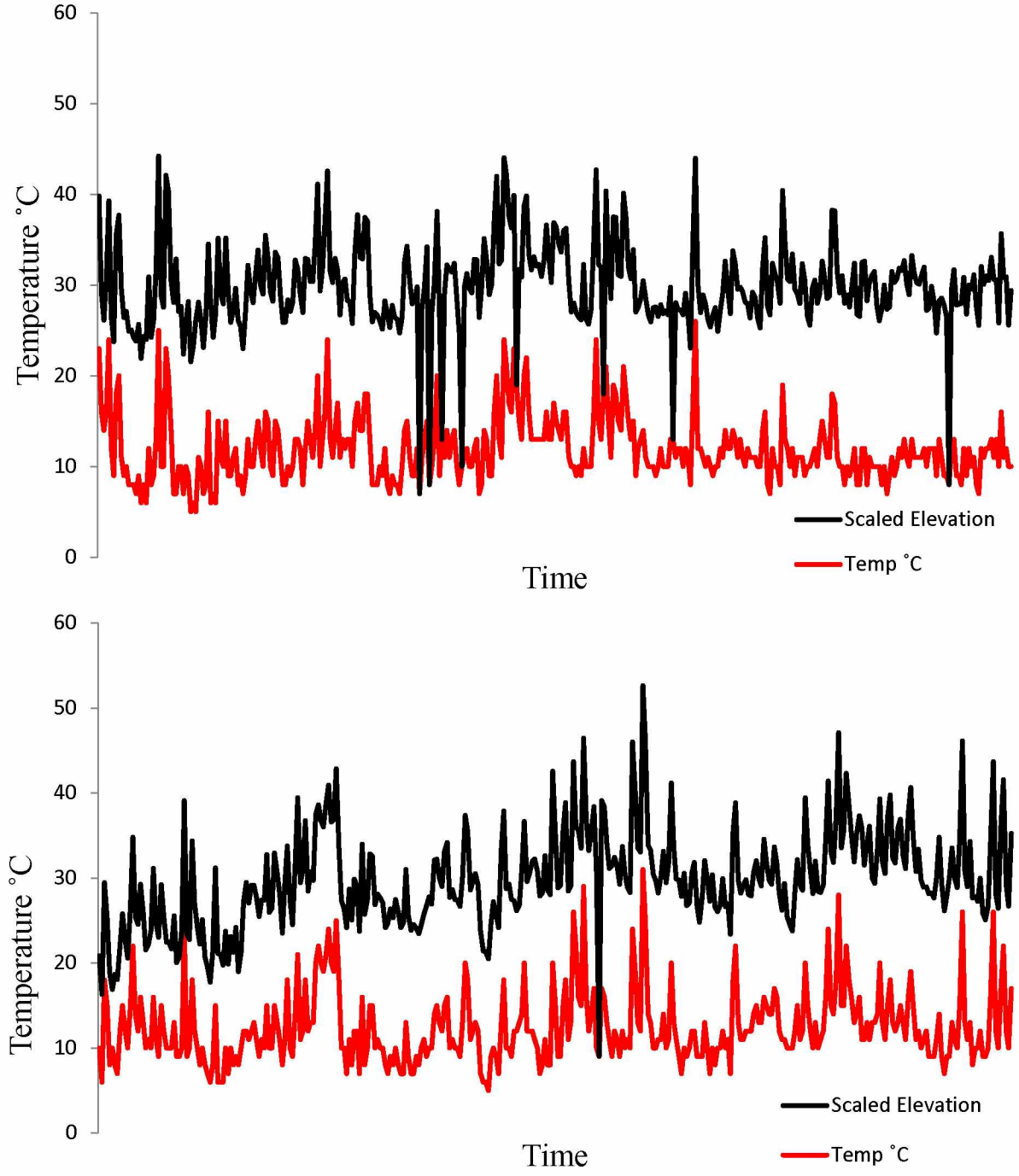

Figure 18. Stacked time series of goat elevations and concurrent ambient temperature. Data series were taken from a collared male mountain goat in Berners Bay, Alaska during summer 2011 (top) and summer 2012 (bottom). Elevation data (m) were scaled for presentation purposes and are derived from a GPS radio collar.

For the second collared animal, only one summer of data was available and, as such, we used this opportunity to investigate whether the temperature elevation signal pattern was evident across smaller (monthly) temporal scales. Temperature affected the elevation of the female collared animal, increasing its elevation by 6.10m (0.52 SE) and was highly significant (AIC= 42404, X^2= 128.18, *P*= 2.2e-16, 95% CI= 5.091 to 7.115) compared to the null (Table 5; Figure 19).

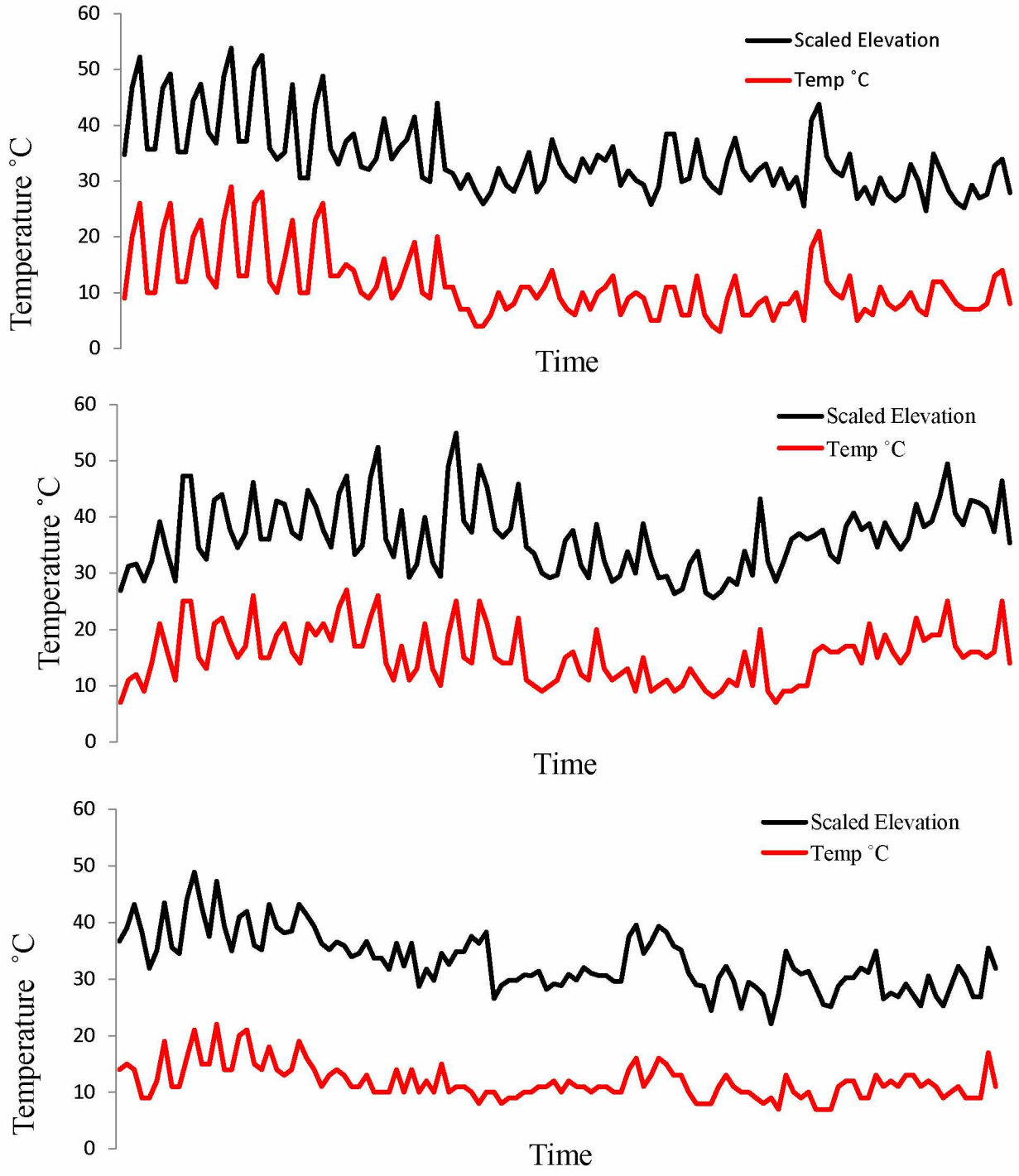

Figure 19. Stacked time series of goat elevations and concurrent ambient temperature. Data series were taken from a collared female mountain goat in Berners Bay, Alaska during summer 2009. Each time series encompasses a single month: June (top), July (middle), and August (bottom.) Elevation data (m) were scaled for presentation purposes and are derived from a GPS radio collar.

Chapter 7 – Discussion

7.1 – Lapse Rate Monitoring

7.1.1 – Daily Near-Surface Lapse Rates

Daily average near-surface lapse rates exhibited high variability from day to day, as is consistent with the literature (e.g., Minder et al., 2010). Variability in mean daily lapse rates was highest during the months of November through January due to the prominence of inversion events. Analysis of mean daily lapse rates underscores the dearth of days in which lapse rates matched the global mean environmental lapse rate of -0.6 to -0.65°C $100m^{-1}$ (Figure 7). Additionally, residual analysis demonstrated that mean daily lapse rate models showed a weak linear relationship between temperature and elevation for the months of November through February. With regard to external validity, I cannot recommend the use of modeled lapse rates for these winter months in Southeast Alaska as an inference tool for temperature at elevation. Even on small spatial scales, the lapse rates measured in Berners Bay demonstrated that basin-scale landscape physiography and topography contribute to spatially unique and unpredictable inversion events. For the months of March through September, residual analysis revealed sufficient model strength to warrant the use of daily mean lapse rates within the Juneau area. The high amount of daily variability in mean near-surface lapse rates measured during this study also suggest that integration of lapse rates to spatially interpolated gridded climate models would be both computationally intensive and challenging. Basin-scale landscape physiographic effects on daily mean lapse rates could easily skew modeling efforts for broader geographic regions and, given a lack of temperature sensor arrays within this region, would likely be quite unrepresentative of local conditions through time.

These findings met my objective to develop a method of statistically modeling monthly mean near-surface lapse rates that could offer climate modelers much more utility toward the effort of regional lapse rate integration into current predictive algorithms. That said, the calculation of daily mean lapse rates could offer novel utility for investigators in the fields of hydrology and ecology. Through the deployment of inexpensive temperature loggers, I have shown that lapse rate calculated over short time scales could lend valuable insight to ecological field investigations. For example, in a region with a dearth of high-quality meteorological stations, ecological investigators could use the daily lapse rate as a reasonable prediction tool for temperature at the elevation of their organism or system of interest (given that investigators know the temperature at sea-level or another elevational reference point). Given day-to-day variability, investigators needing a more accurate temperature estimate could benefit from using a day-specific lapse rate during the spring, summer, and fall, rather than a monthly average. Although synoptic weather types were not investigated here, the documented effect they have on lapse rate

augmentation across short temporal scales suggests that the use of daily mean lapse rates could be more novel in cases where investigators were examining organisms or systems under short term weather conditions. Caution should be exercised, however, in using daily lapse rates for predictive purposes on days that were not included within the study period. The high degree of diel variability highlights that lapse rates are not an accurate prediction of the temperature-elevation relationship on the same day in prior or future years. For such a purpose, monthly mean lapse rates are better suited. Based on these findings, an annual mean lapse rate may have limited utility and could be misleading in many situations.

7.1.2 – Monthly Near-Surface Lapse Rates

Mean monthly near-surface lapse rates demonstrated a yearly sinusoidal pattern, becoming shallower in winter and steeper during the remaining months of the year (Figure 9). Indeed, other studies of lapse rates in south-central Idaho, the Canadian high Arctic, southeast Arizona, Nepal, Ellesmere Island (Canada), the Cascades, the Colorado Rockies, and eastern China have noted this time series topology (Blandford et al., 2008; Gardner et al., 2009; Harlow et al., 2004; Kattel et al., 2013; Marshall et al., 2007; Minder et al., 2010; Pepin and Losleben, 2002; Tang and Fang, 2006). Overall, my results underscore that the use of a generalized mean global environmental lapse rate valued at -0.65°C $100m^{-1}$ (e.g., Barry and Chorley, 1987) is tenuous and non-representative for the dynamic complex terrain system present in Southeast Alaska. Generally, when not corrupted by inversion events, the mean monthly near-surface lapse rate fluctuated between -0.30°C $100m^{-1}$ and -0.45°C $100m^{-1}$. The greatest shift in lapse from one month to the next occurred during the seasonal "transition" months of November and February, whereby the lapse became more rapidly shallow in the former case and more rapidly steep in the latter case (Figure 9). These critical shifts are, again, driven by either the onset or abatement of winter inversion prominence. Additionally, as near-surface temperatures are inexorably linked to surface conditions (e.g., albedo, radiative exposure, snow presence), decreasing lapse rates in the fall and increasing lapse rates in the spring are an artifact of the differential in the surface influence on near-surface temperatures. In both cases, snow may be present (or prevalent) at high elevations, while low-lying areas are snow-free and warm considerably compared to proximal high elevation sites. This dichotomy between near-surface temperatures in snowy terrain and the temperatures measured in snow-free forested areas accentuates the lapse and causes it to steepen or decline rapidly.

My results suggest that models were effective at capturing the seasonal variability of near-surface lapse rates, underscoring the widely published finding (e.g., Blandford et al., 2008) that inversions and cold air pooling, common to mountainous terrains in winter, corrupt the temperature-elevation relationship, in some cases even reversing it (e.g., Minder et al., 2010). My findings support that the prominence of inversion effects on near-surface temperature degrade the inherent existence of a lapse rate

in winter. Though lapse rates are innate to the ideal gas law, covariates within the equation, namely pressures and volumes of air are inexorably augmented during the winter due to the interaction with complex terrain features (i.e., mountains). The magnitude of these pressure-volume gas augmentations are such that cold air masses are driven to pool in montane basins while less dense, warmer air resides above the cold air layer. The strength of seasonal meteorological phenomena to override conventional atmospheric patterns is not just intriguing, but a critical theme for investigators of hydrology, ecology, and climatology to consider when conducting research in mountainous regions. The preponderance of inversion events in winter warrants that elevation should not be used as a proxy for temperature inference during said season. It remains likely that, should my study have been extended over larger temporal scales, I would have captured a complete lapse rate reversal during certain months of a winter.

By calculating monthly mean near-surface lapse rates using linear mixed effects models, I offer a novel improvement to the field of lapse rate analysis. When calculating the monthly means using standard linear regression (as is consistent with the literature), basic statistical model assumptions are often ignored. Using an improved method, I simultaneously mitigated the high day-to-day variability of lapse rates, as well as the spatial and longitudinal pseudoreplication inherent to the data. By treating daily temperature means as points that are allowed to vary within a monthly block sample space, my derivation of mean lapse rates improves overall accuracy. While the mean monthly lapse rates reported here have been measured using only ~1.5 years of data, I expect, given the literature, that these lapse rates are reasonably representative of the average temperature-elevation relationship in Southeast Alaska. As such, investigators should exercise caution when using these reported lapse rates to infer temperature at elevation if the region of interest is outside the Southeast Alaska coastal temperate rainforest system.

This research does well to address one of my primary objectives: to test the validity of the global standard mean environmental lapse rate for use in the Southeast Alaska region. Monthly lapse rates measured in Berners Bay were usually half of the mean global standard (e.g., -0.3˚C $100m^{-1}$ vs. -0.65˚C $100m^{-1}$). This finding highlights the tenuous nature of current spatial interpolation and modeling approaches that may use the mean global standard for predicting or investigating temperatures under climate change scenarios. Near-surface temperatures modeled in this manner for coastal Southeast Alaska (under the mean global standard) are thus a gross overestimate of actual conditions. Resultant scenarios would yield high elevation areas predicted to be much colder than they are in reality, which could generate incorrect assumptions for the myriad of meteorological and ecological metrics common to climate change studies. For example, a lapse rate that is double the actual value has far-reaching conceptual consequences for the understanding of snow persistence, green-up phenology, faunal altitudinal migration and habitat use, altitudinal tree line advancement, and growing degree days. Further,

the extent to which mountains can be thought of as refugia from climate warming extremes may not be as robust as would be assumed under a lapse rate regime of mean -0.65°C $100m^{-1}$.

7.1.3 – Aspect-Level Near-Surface Lapse Rates

My results from Southeast Alaska are consistent with the paradigm that near-surface temperature lapse rates can demonstrate differentiation among aspects of a slope, depending on the season in which they are measured (Lundquist and Cayan, 2007; Tang and Fang, 2006). For example, Tang and Fang (2006) reported consistently lower lapse rates on southerly-facing slopes versus northerly-facing slopes, generally noting a -0.20°C $100m^{-1}$ between aspects over the course of a year. When monthly mean lapse rates from Berners Bay were demarcated by aspect, interesting seasonal patterns became apparent. Lapse rates were congruent for most of the study period, with apparent synoptic weather and radiative exposure-driven anomalies occurring in spring. Local weather systems are dominantly driven by the North Pacific Current meeting mainland North America, forming the northward-flowing Alaska Current. This counterclockwise gyre in the Gulf of Alaska results in weather systems movement from south to north, inherently affecting southerly slopes first, while northern-aspect slopes are more sheltered. The results from aspect-level lapse rate calculations show a clear diversion in the pattern of lapse rate behavior between south/east and north/west aspects (Figure 9). In spring, the lapse rate on south- and east-facing slopes was markedly steeper than the north- or west-facing slopes. By mid-summer the lapse rates across aspects generally converged, though it is notable that the lapse rate on the south-facing aspect was generally steepest year-round. Windier, more weather-exposed south-facing slopes likely experienced stronger, more rapid vertical mixing and orographic uplift, resulting in steeper lapse rates than those that occurred on north and west facing slopes. In April of 2014, an anomaly occurred in which the lapse rate on the east facing transect sharply decreased and then increased to the steepest average lapse measured during this study. This interesting observation highlights the potential for site-specific anomalies within lapse rate investigations, and further, offers an example of why investigators should refrain from reporting lapse rates based on data from very few weather stations (or sensors), or data from a single site (rather than a broader, spatially comprehensive sampling area). The differential between high-elevation sensors that recently emerged from the snowpack and low-elevation sensors within a snow-free forest likely contributed to the observation of this anomaly. Inferences made from lapse rates calculated under such conditions are potentially subject to error as demonstrated by my aspect-level findings.

7.1.4 – Near-Surface Lapse Rates and Implications for Climate Change

Although the existence of a lapse rate is fundamentally rooted in the ideal gas law, I described that near-surface lapse rates are spatially and temporally variable due to physical controls, local landscape

physiography, synoptic weather type, and radiative input. As many of these factors will potentially be augmented by warming global temperatures in the future, it is important to ask the question "Will near-surface lapse rates change with a changing climate?" and further, "How will they change?" Addressing these questions is indeed complex, and much like the high degree of differentiation between regional lapse rates reported in the literature, any future change in near surface lapse rates may be unique to a given region. As previously mentioned, free air temperatures are more stable than near-surface temperatures because of a smaller influence of radiative input. Surface temperatures are ubiquitously warming faster than free air, and although higher elevation mountainous areas (> 3000 m) can demonstrate lapse rates similar to that of free air, changes in radiative forcings with climate change suggest a possible decoupling of the near-surface and free air (Pepin and Losleben, 2002; Pepin and Seidel, 2005). Pepin (2001) found that daytime near-surface lapse rates in northern England steepened over a 30 year time span, while nighttime lapse rates weakened. Similar results were described in the Rocky Mountains of the United States, where lapse rates increased over time especially in conjunction with a higher frequency of westerly synoptic types (Pepin and Losleben, 2002). A global assessment of surface temperatures over the last century conducted by Diaz and Bradley (1997) also suggested a trend of lapse rate increase. Warm surface temperatures can certainly decrease snow volume in mountainous regions, especially at low elevations. The differential, then, in near-surface temperatures at snow-free low elevation sites and proximal high elevation sites that experience near-surface cooling due to persistent snow, can result in increased lapse rates (Scally, 1997). Contrasting results have also been reported though. Pepin et al. (1999) described weaker lapse rates in England during periods of warm temperatures and suggested a warming climate may induce an overall weakening of lapse rates. Summer lapse rates measured in China from 1962 to 2011 also decreased with higher near-surface temperatures, though the opposite was found during all other seasons (Li et al., 2013). Near-surface lapse rates for the Tibetan Plateau are expected to weaken overall with global warming (Li et al., 2013). In Alaska, Dial et al. (2015) found no change in summer lapse rates measured in the Anchorage area from 1972 to 2012.

With such contrasting suggestions as to the possible evolution of lapse rates through time, and the regional variability with which lapse rates measured across temporal scales have been described, perhaps a more constructive approach is to predict the lapse rate change based on more fundamental and well-established factors. For example, it is widely accepted that near-surface lapse rates are lower with increased humidity when compared to arid conditions (Du et al., 2010; Kattel et al., 2013; Li et al., 2013; Pepin et al., 1999; Tang and Fang, 2006). Indeed, results of this study demonstrated that near-surface lapse rates in the coastal temperate rainforest of Southeast Alaska are most similar to a moist adiabatic lapse rate (often weaker, in fact) and nearly half that of the global mean. Likewise, near-surface lapse rates during the monsoon season in the central Himalaya and Tibetan Plateau are seasonally the lowest

and have exhibited a decreasing trend over time (Du et al., 2010; Kattel et al., 2013; Li et al., 2013). Nearby, eastern China also demonstrates this trend (Tang and Fang, 2006). As water is perpetually released from the cryosphere under a warming climate, hydrologic fluxes are widely projected to increase the amount of moisture in Earth's atmosphere, elevating global precipitation levels. Conceptually, theory dictates that latent heat is released as water condenses at high elevations in mountainous areas, thus, warming near-surface air and weakening the lapse rate (Kattel et al., 2013). Increased cloudiness and humidity coupled with warming scenarios is generally expected to decrease near-surface lapse rates, as exemplified by the expectation of sharply decreased lapse rates in the tropics (Kattel et al., 2013; Pepin et al., 1999).

An important consideration when attempting to actualize lapse rate behavior under climate warming scenarios is that the temperature regimes of different geographic regions may vary with regard to the effects of higher greenhouse gas concentrations (Pepin et al., 1999). Moreover, they will also vary as a result of perpetual change to the physical structure of the atmosphere itself (Pepin et al., 1999). As such, it is imperative that near-surface lapse rates be monitored regionally to produce accurate estimations of temperature-elevation relationships in mountainous regions. The combined effect of changing atmospheric circulation patterns, atmospheric structure, increased regional radiative forcings, and shifting synoptic types on spatial temperature distributions warrants that to address the issue of potentially evolving lapse rates, spatial interpolation models must take downscaled regional lapse rates into account, rather than relying on a global average. Climate is a conglomerate of many interacting and non-mutually exclusive factors. Climate change involves positive feedbacks associated with: melting snow, glaciers, permafrost, the northward migration of the boreal forest and concurrent extirpation of the tundra, changes in energy and hydrologic fluxes between the terrestrial realm and the atmosphere, and the uncertain magnitude of anthropogenic exacerbation. Unequivocally, it remains difficult to pinpoint whether a general rule for the evolution of lapse rates exists; however, the unanimous presence of warming surface temperatures, increased greenhouse gas concentrations, and increasing precipitation suggests that if all the previously mentioned factors are changing, near-surface lapse rates will too. All else being equal, unchanged lapse rates in the future still translate to warmer temperatures in sub-alpine and alpine regions that will irrevocably alter the structure, function, and phenology of ecosystems.

Due to the same fundamental physical controls, near-surface lapse rates in the coastal temperate rainforest of Southeast Alaska may decrease with increased surface temperatures, as is predicted for the tropics. Recent global analyses of average surface temperature warming between 1948 and 2002 not only highlight that mean warming is significantly higher at high latitudes, but Alaska and Canada are among the few regions (globally) that exhibit the highest geographic concentration of surface temperature warming (Pepin and Seidel, 2005). Recent downscaled modeling efforts for the region revealed that the

annual mean temperature in the coastal temperate rainforest may increase up to ~4°C for the IPCC Representative Concentration Pathway (RCP) 4.5 and up to ~6°C for RCP8.5 by the year 2100 (Shanley et al., 2015). Mean annual precipitation may increase up to 9% for RCP4.5 and up to 18% for RCP8.5, while total annual precipitation falling as snow may decrease up to 40% for RCP4.5 and up to 58% for RCP8.5 by the year 2100 (Shanley et al., 2015). Taken together, increased precipitation (with assumed associated increased cloudiness), and increased surface temperatures in a region already defined by high humidity, a maritime climate, and moist adiabatic (or weaker) lapse rates, suggests a regional weakening of near-surface lapse rates is a reasonable prediction. This is not to say, however, that such a trend would be pervasive across Alaska, as the state can be broken up into 13 climate divisions, each based on unique local topography, latitude, and proximity to oceans (Bieniek et al., 2012).

7.1.5 – Thermal Dynamics Implications for Ecosystem and Biotic Conservation

Well established implications and areas of interest regarding climate change effects on montane ecosystems and biota include: thermal thresholds and heat tolerances; latitudinal and elevational shifts in species ranges and distributions; changes to ecosystem structure and function; population contractions and expansions; increased interspecific competition for resources; alterations of demographics and predation risk for wildlife; and biodiversity loss. As temperature and climate variation have indeed influenced evolutionary adaptation, biotic life histories, and distributions of species through time, the yet-to-be determined resilience of various species and ecosystems is of particular concern (Mawdsley et al., 2009). Given that the current velocity of climate change may be altered under different potential warming scenarios, it remains imperative to assess the capability of species and systems to adapt in time (Kelly et al., 2007; Loarie et al., 2009). For studies in montane regions, the aforementioned topics of concern rarely include explicit consideration or mention of biotic interactions with, or consequences of lapse rates. Further, the scant examples contain varying degrees of robustness (e.g., Grabherr et al., 1994; Prentice et al., 1992; Richardson et al., 2004; Wang et al., 2012a). Near-surface lapse rates are, in fact, at the forefront of ecological and biotic importance in mountainous regions though.

Temperature and thermal gradients in mountainous regions have substantial impacts on vegetative communities. Fundamentally, temperature is a primary mechanism driving plant physiology, structural growth, photosynthetic capability, evapotranspiration, and spatial range extent (Korner and Paulsen, 2004). In mountainous environments, spatial extent of surface temperatures denotes the presence and elevation of treeline (Korner and Paulsen, 2004). As a result of warming surface and near-surface air temperatures, high latitude mountainous regions are widely described to experience a loss of alpine habitat with concurrent elevational expansion of forest and treeline (DellaSala et al., 2011; Mountain Research Initiative, 2015; Shanley et al., 2015; Wang et al., 2012; Wang et al., 2012a). Both the presence

of a thermal threshold for treeline and the rate of elevational vegetative advancement under a warming climate will inevitably depend on local lapse rates in a given region. Further, under a scenario of weakening lapse rates, the rate of elevational expansion and treeline advancement will be bolstered by a decrease in cool temperatures at high elevations, thus hastening the disappearance of the alpine. The degree to which investigators can accurately predict or model such vegetative changes in regions of interest will inevitably depend on the level of downscaling achieved in future studies, as well as the accurate estimation of local lapse rates. Winter snow accumulation, annual persistence, and melt phenology are also of particular importance to mountain vegetative communities, and warrant consideration of near-surface lapse rates. In the coastal temperate rainforest, the coupling of increased mean annual temperature and precipitation with a projected simultaneous decrease in annual snow volume precipitates in the expansion or contraction of montane tree species distributions. Observational and modeling studies agree on the proliferation of western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) under warming scenarios, while species such as mountain hemlock (*Tsuga mertensiana*) will experience notable contractions (DellaSala et al., 2011; Shanley et al., 2015; Wang et al., 2012a). Without a doubt, seasonal snow persistence, melt timing, and melt rates depend on a thermal threshold of 0°C temperature as it spatially occurs on a slope. Additionally, lower snow years and increased temperatures in the coastal temperate rainforest will drive earlier green-up and precipitate an increase in growing degree days. Lapse rates are inherent and fundamental to these vegetative shifts, and as such, investigators attempting to estimate future vegetative community changes would be wise to incorporate near-surface lapse rates as a critical abiotic metric within their models and/or observational studies. Though I can only speculate the prediction of weakening lapse rates in Southeast Alaska, consideration of regional average lapses like the ones reported here will aid in the understanding of how they serve to buffer warming at high elevations, and contribute to the proliferation or extirpation of floral species.

Thermal gradients in complex terrain are also of crucial importance to wildlife in the face of a warming climate. Not only have shifting species distributions already been reported, but projections of biodiversity loss even under low emissions scenarios will undoubtedly augment the structure and function of biotic communities (Lawler et al., 2009). Rubidge et al. (2012) found that a 3°C increase in temperature in the Sierra Nevada during the last century induced an elevational increase in the lower limit of alpine chipmunk (*Tamias alpinus*) distribution by more than 500m, vastly contracting the species' spatial range. The investigators comprehensively highlighted the biological magnitude of this range contraction by simultaneously measuring a substantial decrease in *T. alpinus* genetic diversity, and forecasted the potential for species extinction due to reduced adaptive potential and increased inbreeding depression. In this example (although not explicitly stated), habitat use and thermal tolerance for this

species is intimately linked with near-surface lapse rates. A more exhaustive approach to this research could have been the addition of regional near-surface lapse rates, like those described by Lundquist and Cayan, (2007) for the same study area. Adding lapse rate data to this analysis would enable the authors to produce both a compelling account and validation of thermal thresholds for this species and reveal climate warming induced interactions between the animals, their habitat, their life history, and their resource use. To that end, novel findings of climate driven genetic erosion and species persistence could be demonstrated to possess a key linkage with near-surface lapse rates and alpine thermal gradients.

Understanding the potential for species loss and shifting distributions can also be improved by near-surface lapse rates by incorporating them into spatial climate models to increase the accuracy of environmental change predictions. As lapse rates can be used within models to inform estimates of glacial ablation rates or snow persistence and melt timing, organisms that rely on sensitive and disappearing habitats in mountainous regions are again, intimately linked to thermal gradients. For example, modeling of glacier mass balance and snow melt in the northern Rocky Mountains predicts a high probability of extinction for the meltwater stonefly (*Lednia tumana*) (Muhlfeld et al., 2011). This species has an extremely restricted range and is currently a candidate for listing under the US Endangered Species Act. The plight of this aquatic invertebrate is important as listing will mark only the second species to ever be listed as a direct result of climate change (the only current such species is the polar bear (*Ursus maritimus*) (Muhlfeld et al., 2011). This exemplar highlights how thermal gradients, spatial interpolation modeling, and increased accuracy in montane hydrologic change estimation due to lapse rate inclusion can significantly impact wildlife conservation. Indeed, sensitive species such as this can serve as early warning indicators for climate induced ecosystem change and biodiversity loss. Analogs of potentially threatened indicator species affected by lapse rate behavior within the coastal temperate rainforest are the Staphylinid beetles of genus *Phlaeopterus*. These alpine invertebrates both scavenge and prey upon other insects at the terminus of persistent snow patches in summer (L. Mullen, pers. comm.). As lapse rates serve as a final buffer against warming surface temperatures that deplete persistent snow patches in summer, considerations of regional lapse rates can aid in the assessment of potential range contractions, alterations of food web dynamics/trophic interactions of alpine invertebrate, and the identification of enigmatic, under-described climate change indicator species (L. Mullen, pers. comm.). Again, the ability to accurately evaluate climate interactions with sensitive biota and measure changes in ecosystem structure requires appropriate downscaling and considerations of near-surface lapse rates specific to the coastal temperate rainforest. My results represent a meaningful first step towards this effort.

7.2 – Mountain Goat Behavioral Monitoring

7.2.1 – Mountain Goat Activity on Warm and Cool Days

Linear mixed models testing the effect of temperature on male and female activity budgets revealed that there was no (statistically) significant augmentation of time spent bedded or feeding between hot and cool days. This finding was in direct contradiction of my first study prediction: the animals would increase time spent bedded and decrease time spent feeding on warm days as a behavioral thermoregulatory mechanism. Although the temperature signal existed, it was not statistically significant for time spent feeding or bedded. Generally, the opposition of time spent feeding and bedded for both male and female mountain goats agrees with previous behavioral studies conducted on goats in Alberta, Canada by Hamel and Côté (2007) and Mainguy and Côté (2008). The result of a weak, yet present temperature effect at my temperature categories (< or > 15˚C) could potentially have been the result of low temporal scale measurement. Further, summers in Southeast Alaska are generally cool, and an ambient temperature threshold of >15˚C to denote conditions for heat stress may have been too conservative. This raises a question as to whether restructuring the data to reflect a higher demarcation point (e.g., 20 – 23˚C) would result in a statistically significant effect of temperature on behavior. An issue with augmenting the analysis in this way is that the highest monthly maximum temperature for May through August during the study period was only 17.3˚C. Daily maximum temperatures at or above 20˚C are uncommon throughout the summer in this region. The short duration of my sampling effort and the dearth of days where a higher threshold temperature (than those established in the literature) could be sampled makes such an effort unfeasible. Of the two summers mountain goats were observed, the majority of behavioral data collected took place during the summer of 2014, which happened to be one of the coolest summers on record for the Juneau area. Further, from June – September 2014, the greater Juneau area received the highest monthly precipitation levels ever recorded. This likely contributed to the relatively constant proportions of feeding that I observed, rather than revealing a stark dichotomy between the percentages of time spent feeding and bedding on warm and cool days. Weather conditions aside, the data suggest that augmentation of the activity budget by trading off foraging for bedding may not be a primary thermoregulatory mechanism, decoupled from other factors/strategies. It is important to note that the statistical models used in this study incorporated three temperature variables including temperature at the time of survey, maximum daily temperature, and warm/cool day. None significantly affected behavioral proportions by themselves. Again, this result was surprising as some of the closest analog ungulates for comparison, alpine chamois and alpine ibex, have been described to markedly decrease feeding time in association with hot temperatures (Aublet et al., 2009; Mason et al., 2014a). That said, in

the case of ibex studied by Aublet et al. (2009), it remains unclear whether or not modification of the activity budget was simultaneously owed to high temperatures while decoupled with period of day or elevational adjustments. High ambient temperatures unequivocally affect both ungulate behavior and habitat selection: modifying activity budgets in female mountain goats (Hamel and Côté, 2007), decreasing body condition or increasing thermal cover selection for moose (Van Beest and Milner, 2013), augmenting behavior and decreasing body mass in alpine chamois populations (Mason et al., 2014; Rughetti and Festa-Bianchet, 2012), and influencing habitat use and activity budgets in alpine ibex (Aublet et al., 2009). My first investigation though, certainly suggests the relationship between temperature and mountain goat activity within the study area involves interplay of a more complex nature.

7.2.2 – Period of Day as a Determinant of Mountain Goat Activity

The PCA-derived result of opposition of feeding and bedding behavior being the cardinal feature of mountain goat activity is rather pervasive across ungulates; abridged examples including: ibex, muskoxen (*Ovibos moshatus*), wildebeest (*Connochaetes gnou*), steenbok, and kudu (Aublet et al., 2009; Côté et al., 1997; Du Toit and Yetman, 2005; Maloney et al., 2005). For both sampling methods exercised here, the opposition of feeding and bedding behavior explained a third of the variation of all goat activity. Even more ubiquitous though, is the description of ungulates reducing time feeding at midday, increasing bedding time at midday, and concurrently trading-off time actively feeding for cooler periods (morning and evening). This behavioral trait is especially prevalent among ungulates in more arid climes, where intense daytime temperatures relegate desert bighorn sheep (*Ovis canadensis nelsoni*), topi (*Damaliscus korrigum*), mule deer (*Odocoileus hemionus*), and wildebeest to resting until crepuscular feeding ensues (Alderman et al., 1989; Cain et al., 2006; Maloney et al., 2005; Sargeant et al., 1994; Vrahimis and Kok, 1992). The behavioral thermoregulatory dichotomy between resting during midday and feeding during both morning and evening periods has been described for goitred gazelles (*Gazella subgutturosa*), steenbok, kudu, and mountain reedbuck (*Redunca fulvorufula*) (Du Toit and Yetman, 2005; Roberts and Dunbar, 1991; Xia et al., 2011). Temperate ungulates also maintain this strategy, for example, the foraging behavior of elk in the Rocky Mountains takes place in the morning and evening throughout the entire year (Green and Bear, 1990). Festa-Bianchet (1988) notes bighorn sheep inhabiting relatively low elevation (~1500m) ranges in summer restrict feeding bouts to morning and evening, while during midday the animals were observed panting (both a sign of extreme heat stress and an energetically costly mode of thermoregulation). Further compelling findings from that study noted a trade-off, in that nearby populations of sheep selecting a higher elevation summer range in the alpine (~1800 – 2500m) did not demonstrate this behavior, and instead spent more time foraging in cooler habitat (though forage availability was much lower) (Festa-Bianchet, 1988).

The significant influence of period of day on mountain goat activity has elsewhere been described for the extensively monitored (1989 – present) population in Caw Ridge, Alberta, Canada (Festa-Bianchet and Côté, 2008; Hamel and Côté, 2007). Corroborating my findings, a four-summer scan sampling behavioral study of ~50 – 60 collared females revealed that the specific period of day adjustment for female foraging (versus bedding) was, as this study found, in the evening. Most strikingly, despite the short duration of the sampling period (~1.5 summers) in Berners Bay, female mountain goats within the study area were also found to exhibit roughly 50% more feeding time than percentages measured at midday and in the morning, as was the case at Caw Ridge. In the Caw Ridge study, maximum daily temperature was indeed found to be a statistically significant indicator (along with period of day) affecting activity budgets, whereas it was not in this study. This discrepancy could have again been due to a shorter temporal sampling effort encompassing a summer of unusually high precipitation and cold weather during 2014, even for Southeast Alaska. Nevertheless, it remains compelling that my original prediction of significantly high bedding and low feeding during warm weather days (and vice versa) is rejected in favor of mountain goats maintaining roughly the same budget across variable temperature days, yet shifting its orientation through time to compensate.

Given the outcome of LMM analysis on the feeding versus standing behavioral opposition, my results suggest a sexual dichotomy between potential trade-offs in terms of behavioral life history strategies. Taken together, during the two periods of day in which males reduced feeding, they increased (by double) the amount of standing for both periods, including midday. Females on the other hand, only increased standing in the morning and favored bedding during midday. According to the scan results, they did not change the proportion of standing behavior on warm or cool days, and generally stood half as much as males did; whereas males doubled the proportion of standing behavior on warm days. As females aggregate in large nanny-kid groups, a potential explanation for the behavioral tendencies observed here could be an energetic and fitness benefit for females bedding together during the warmest parts of the day. In doing so, they reduce activity and energy expenditure, allow time for rumination, and increase protection from predators for both adult females with and without young. Females in summer have greater metabolic and energetic demands due to gestation, lactation, and personal optimum forage in preparation for winter compared to that of males, so energetic conservation during midday (found across the entirety of my results) appears to be a valid assumption. Males though, as generally solitary animals may demonstrate a different strategy by finding a shady or high elevation site to stand and ruminate during the warmest parts of the day. Males would likewise not have the benefit of many individuals bedded together in different spatial orientations, which increases visibility of the landscape, acting in favor of predator avoidance/detection for the group. As such, perhaps it pays as a solitary individual to occupy a site during midday in a standing position to mitigate the increased chances of potential predator interactions while

inactive and engaging in homeothermic effort. The amount of heat generated while standing in cattle has been described to be 1/5 of that generated while engaged in feeding behavior (Aublet et al., 2009; Malechek and Smith, 1976). Though they are exposed to much greater temperatures, steenbok, impala, kudu, and giraffes investigated by Du Toit and Yetman (2005) demonstrated resting while standing (with concurrent decreases in feeding) as a thermoregulatory mechanism in response to maximum daily temperature. As mountain goats are the least studied North American ungulate, little explanation exists for species-specific trade-offs in terms of feeding versus standing behavior in males (Festa-Bianchet and Côté, 2008). Mainguy and Côté (2008) suggest the opposition of feeding and standing behavior is a critical facet of male activity budgets during the rut to facilitate sightability of potential mates and rival males; however, this is not the case in summer. Often, on warm cloudless days, solitary males could be observed at my study site at high elevation crags, standing in the shade (pers. obs.). Though I could not initially be sure of an exact strategy to explain this male behavioral opposition, given that standing is traded off for feeding (i.e., in the absence of optimum foraging theory), the two most plausible explanations based on mountain goat life history would be predator avoidance and thermoregulation. A similar occurrence was noted in black wildebeest and antelope activity budgets, and it was postulated that for African ruminants, late-day thermal loading was most contributed to by radiation coming from the ground surface, rather than overhead (Finch, 1972; Maloney et al., 2005). For alpine ungulates though, a standing posture at high elevation (where it is cooler), would increase the surface area of the animal exposed to the environment, allowing for greater ease of heat dissipation. Not only would selecting for shady microclimates reduce head loading in late day, but convective cooling is also bolstered in standing ungulates simply based on body orientation relative to the sun or wind (Cain et al., 2006), Indeed, advances in the field of endotherm energetics for ungulates underscores the importance of behavioral selection of microclimatic shading and alteration of body posture as critical strategies for the maintenance of homeothermy and inhibition of heat stress (Dudley et al., 2013; Natori and Porter, 2007; Porter et al., 2002).

7.2.3 – Temperature Effects on Mountain Goat Elevation and Habitat Use

Results of the analysis on the effect of temperature on mountain goat elevation revealed a strikingly coupled relationship between mountain goat behavior, homeothermic maintenance, and habitat selection. I confirmed a consistent relationship between mountain goat elevation depending on the temperature that the animal experiences. That said, I can only suggest this particular relationship's magnitude for the mountain goats in the study area. As this relationship has yet to be investigated by other researchers for mountain goats throughout their range, it remains possible that local climate conditions, topographic and altitudinal complexity, behavioral and homeothermic plasticity, and isolation by distance

may cause regional difference in the precise value of elevational mountain goat movement due to temperature.

Research has confirmed that across a range of ungulate species, animals engage in both specialized habitat selection and movement as a thermoregulatory strategy. Even in temperate regions, ungulates such as moose, serow, and goral (*Naemorhedus caudatus*) have been shown to alter their habitat selection in favor of shaded areas (such as forest or rock cover) within their habitat as a thermoregulatory mechanism during summers when excessive heat loading potential is common (Buranapim et al., 2014; Schwab and Pitt, 1991; Van Beest et al., 2012). Niche specialization by alpine ungulates, however, may render them incapable of accessing forested cover during the summer as respective ranges where forage is abundant exist above tree line. Amelioration of heat stress by making daily altitudinal movements during hot days seems to be a common strategy across alpine ungulate species in particular. Alpine chamois, one of the closest genetic relatives of mountain goats have been shown to both alter their activity budgets and make daily elevational movements on hot days (Festa-Bianchet and Côté, 2008; Mason et al., 2014). A two-year study of female alpine ibex home-range size and spatial habitat use in the Italian Alps demonstrated vastly different magnitudes of space use between warm and cool years (Grignolio et al., 2004). Collared female ibex during the warmer year (2001) altered their habitat use by an average increase of ~1000 m in both spring and summer. Further, altitudinal movements occurred daily, as the animals would move to high elevation sites in the morning and descend in the evening when warm daytime temperatures abated. Similar results were found in male ibex within the same study area (Aublet et al., 2009). Male ibex demonstrated consistent elevational gain up to 800m on warm days – resting during midday, whereas during cool days they did not engage in altitudinal movements and fed across all periods of the day (Aublet et al., 2009).

These results demonstrate clear interaction between temperature and mountain goat elevation. Both focal and scan sampled goats consistently mediated the elevation of habitat they used in conjunction with changes in temperature (Figure 16). Confirmation of this pattern was done using two data sets from collared individuals within the study area, but in years prior to my behavioral monitoring/presence (Figure 17, Figure 18). Even though measurements from within-collar thermistors are likely affected somewhat by the body heat of the animal, the pattern was still clearly evident, suggesting that the temperature data from the collar was a viable proxy for estimating the existence of the relationship. Mountain goats made elevational increases or decreases based on increases or decreases in ambient temperature. As has been observed with European alpine ungulates, mountain goats in Southeast Alaska seem to be using elevational temperature shift (near-surface lapse rates) as a thermoregulatory mechanism to ensure homeothermic maintenance. To my knowledge this is the first time this relationship has been explicitly described for this species. Further, whereas ibex and chamois have demonstrated this trend in a

general sense across daily and monthly scales, my findings are unique to all of ungulate ecology, in that, this phenomenon is occurring seemingly independent of behavior (as was not the case for the European analogs). Results show that, in general, mountain goat elevation is altered ~6-7m for every degree Celsius change in temperature during summer. All linear mixed effects models were highly significant and the pattern was evident throughout all months of the summer for which data were collected. The pattern shows that a mountain goat would vertically shift its elevation, independent of all other factors, ~90m between temperatures at the high end of those experienced for this region in summer and those on a cool summer day. Near-surface lapse rates measured in the study area averaged $0.4^{\circ}C\ 100m^{-1}$. Interestingly, the mountain goats in Berners Bay shift their spatial orientation on the landscape by ~1.5 - 1.75 times the lapse rate throughout the day and further, perpetually throughout the summer. Considering the aforementioned findings, I hypothesize that this elevational movement in concert with the air temperature lapse rate results in maintenance of thermoneutrality. Given the complexity of climate, atmospheric physics, and meteorology, the use of lapse rates by a wildlife species as a continuous thermoregulatory strategy is certainly a most fascinating finding. To my knowledge, this as well has never been described.

7.2.4 – On the Nexus of Eco-physiology, Behavior, Climate, and the Future

Climate is unequivocally changing. As global surface temperatures warm, ecosystems and the species therein are at risk of extirpation. Understanding the change in function and structure of ecosystems is critical to wildlife research and conservation efforts, especially in Alaska. A novel approach to understanding the true scope of system change is the use of indicator species, those whose marked interaction with the biotic and abiotic components of systems transcends climatic, habitat, and temporal gradients. Measuring indicator species' life history, behavior, ecology, and physiology can lend profound amounts of understanding toward the trajectory of change for whole systems. As climate change is predicted to have stronger impacts on northern latitudes and alpine environments, mountain goats and other alpine ungulates are critical sentinel species for wildlife ecology research and conservation.

Although there is a current dearth of alpine ungulate studies taking a comprehensive approach to physiology, behavior, and climate, research from the Italian Alps has shown that ibex and chamois demonstrate notable reactions to heat stress, first by altering the proportion of time spent engaging in feeding behavior, and second, by making elevational movements to compensate for thermal stress. Notably, behavioral shifts are generally expected to predominate, as I expected to find for mountain goats in Berners Bay. These results point out that although increases in temperature, even when investigated across short temporal scales affect mountain goat behavior, both the mechanisms driving the change and the resultant consequences may not be easily decipherable. During this study, mountain goats were not found to overwhelmingly alter the proportions of time spent in various activities as a result of ambient

temperature shifts. They enacted roughly the same budgets, while instead, shifting their orientation through space and time. This strategy has obvious benefits for maintaining the activity levels required to garner nutritional resources over the course of the summer. Mountain ungulates in Europe and Asia for example, can increase their daily elevation gain by as much as 800m when heat-stressed. In addition, they reduce time feeding in favor of bedding so as not to exert additional energy (Aublet et al., 2009; Mason et al., 2014). In Southeast Alaska, the maximum elevational extent for much of the montane habitat is only 1500m asl. Tree line at the mountain goat observation sites was at roughly 800 m asl. As I routinely observed mountain goats at the highest extent of their habitat, it doesn't appear they have much more elevational space-use with which to mitigate heat stress, should temperatures warm. Mountain goats on Kodiak Island and the Kenai Mountains were also most often observed to inhabit the highest elevational extent of their range in summer (Hjeljord, 1973). My results demonstrate the critical linkage of mountain goat physiological responses to temperature increases – manifested through behavioral habitat selection. The goats appear to be shifting their feeding times to early or late periods of the day, while also keying into near-surface lapse rates to maintain homeothermy. This suggests that mountain goats may be quite behaviorally plastic, and may need to be, as a function of the harsh conditions in which they live (Aublet et al., 2009; Festa-Bianchet and Côté, 2008; Hjeljord, 1973; Mason et al., 2014a). In terms of feeding, mountain goats have been described as "selective generalists", foraging on a variety of forbs and graminoids (Cobb et al., 2012; Festa-Bianchet and Côté, 2008). Perhaps they act in a similar way in terms of habitat and space use. Facing warming temperatures in their habitat, the behavioral responses I found beg the question "Will mountain goats shift their activity to even later periods of the day, demonstrating a more crepuscular budget as the African ruminants do?" Will mountain goats simply increase the factor by which they make elevational movements and continue to "surf" the near-surface lapse rate? Mountain goats within the study area did not appear to feed at night (at least currently). Further, given the behavioral plasticity of the animals, why then, is survival lower in Southeast Alaska mountain goat populations following warm summers? Many studies have shown that plant nutrition decreases in sunnier, hotter conditions (Albon and Langvatn, 1992; Fox, 1991; Mason et al., 2014a; Mysterud et al., 2001; Seip and Bunnell, 1985). It remains likely that even a high abundance of low quality forage will be detrimental to mountain goat nutrition and survival if warming trends continue. Mountain goats in this area also show seasonal altitudinal movement, following new, nutritious growth uphill as it emerges from snow (even through summer at high elevation sites). Bischof et al. (2012) described this tendency in ungulates as "surfing the green wave…in pursuit of spring". Early plant phonological senescence due to increased rainfall and warming temperatures (both predicted for Southeast Alaska, even under low emissions scenarios) will certainly reduce digestibility and nutrient (e.g., crude protein and nitrogen) content for alpine forbs and graminoids (Fox, 1991; Giorgi et al., 1997; Lenart et al., 2002; Pepin and Seidel, 2005;

Pettorelli et al., 2007; Shanley et al., 2015). Further, tree line is moving upslope while concurrently the percent alpine is shrinking (DellaSala et al., 2011; Mountain Research Initiative, 2015; Shanley et al., 2015; Wang et al., 2012; Wang et al., 2012a). These amalgamating factors do not intuitively suggest an improvement in mountain goat survival. That said, higher amounts of precipitation and increased cloudiness may bode well for the species being able to engage in thermoregulatory maintenance.

Mason et al. (2014) compellingly found that alpine chamois in the Alps are losing body mass over time with increases in warmer temperatures during summer. This may be linked to decreases in body condition due to heat stress and/or sub-optimal forage. Likewise, environmental changes due to climate have caused 5% reductions in body size (both mass and shorter limbs) over the last 20 years in Soay sheep (*Ovis aries*; Ozgul et al., 2009). Physiologically though, larger-bodied endotherms have higher energetic and metabolic costs than smaller ones (Mysterud et al., 2001; Porter et al., 2000; Porter et al., 2002). When weighing the interplay of climate, physiology, and behavior with respect to foraging, three canons of note should be considered: optimum foraging theory, the marginal value theorem, and (to a lesser extent) Bergmann's rule. If mountain goats are augmenting their behavior and life history to retrieve maximum nutritional gains while expending the least amount of energetic/physiological cost, it makes sense to optimize their activity budget by foraging in such a way that reduces exacerbating losses such as heat stress; thus, the manifestation of an elevational homeothermic balance coupled with resting bouts during warm periods and feeding during cool periods. With low survival demonstrated after warm summers, mountain goat analogs in the Alps demonstrating body mass reductions, and forage quality declining through time (and earlier in the spring) with climate warming, perhaps a reduction in body mass effect will be observed for mountain goats in the coming years. My coupled lapse rate research proposes a probable weakening of near-surface lapse rates in Southeast Alaska with increased anthropogenic global warming. If mountain goats utilize elevational gain and reduction as a mechanism for thermoregulation, the extent to which they do could be heightened. The elevational extent of Southeast Alaskan mountains reaches only ~1500m. My results, when coupled with probable increases in surface temperatures, weakening lapse rates, and diminishing percent alpine, lend support to the hypothesis that alpine obligates may be "pushed off the top of the mountain" after a certain climate threshold is reached.

Often, findings of organismal change as a result of climate lead to sweeping predictions of range contractions, and eventually species extinctions. Species are undeniably going extinct at a rate not seen since the last global mass extinction and must adapt to the velocity of climate change in order to survive (Barnosky et al., 2011; Dirzo and Raven, 2003; Loarie et al., 2009). A compelling thought, however, is that perhaps behaviorally plastic animals such as alpine ungulates are not signaling the onset of population collapse. Indeed, reductions in body mass can be an inference of poor condition in ungulates. In considering Bergmann's rule, we see that cooler temperatures physiologically favor large-bodied

terrestrial vertebrates, as evinced by larger-bodied organisms abounding as one moves toward the poles. If alpine ungulate behavioral plasticity across space and time was not enough to ensure optimality in forage, energetic gains, and cost reduction, selection over the long-term would physiologically favor smaller body size in a warmer environment. History corroborates such a prediction, in that the global thermal maximum (often used as a case study for the current Anthropocene warming event) that occurred in the late Paleocene epoch caused pervasive mammalian reduction in body size by >30% (Jardine, 2011; Long et al., 2013). Though mountain goats are often compared to their analogs, the chamois, serow, ibex, tahr, and goral of Europe and Asia, this is largely a function of the fact that no other alpine "goat-antelope" (i.e., non-sheep) Caprinae exist in North America. Moreover, mountain goats are monotypic, being the sole member of their genus. The ancestral (still-living) form, likely from Alaska has gone relatively unchanged for 100,000 years and exhibits low genetic diversity (Shafer et al., 2012). One other member of this genus is known to have existed, having died out around 10,000 years ago according to the fossil record: *Oreamnos harringtoni* (Mead, 1983). Though little is known about Harrington's mountain goat, the following is evident. This species is a descended lineage of the living form of American mountain goats. It lived in arid regions of the American Southwest and used caves for shelter. Its primary bifurcating morphological characteristic was that it was only 2/3 the size of *Oreamnos americanus*. (Festa-Bianchet and Côté, 2008; Mead, 1983)

Chapter 8 – Conclusions

8.1 – Concluding Remarks on Near-Surface Lapse Rates

Results of near-surface temperature monitoring in Berners Bay demonstrated a clear elevational dependency of temperature across spatiotemporal scales. I described that global climate change may be more pronounced, and more variable at high latitudes. This coupling underscores the need for downscaled, high resolution regional monitoring in a warming world. Southeast Alaska near-surface lapse rates behaved as moist adiabatic lapses; however, monthly average lapse rates were often weaker. The use of a global mean lapse rate to describe or model climate in the complex terrain-dominated coastal temperate rainforest of Southeast Alaska is unwise. Doing so would grossly overestimate the rate of cooling with increased elevation in mountainous environments, and lead investigators to infer temperatures that were, on average, up to 50% cooler across elevational gradients. This finding signifies the importance of regional downscaling and the unique climate of a dynamic and novel temperate rainforest system. In order to fully understand how a changing climate will affect abiotic regimes such as synoptic weather, hydrology, snow extent, and projected near-surface temperature increase, it is imperative to consider accurate near-surface lapse rates as an included metric. As well, climate change-related questions as to the future range expansions or contractions of species, the potential for species extinctions, changes to demography and community structure, and the overall structure, function, and phenology of ecosystems, should take near-surface lapse rates into account. Informing current scientific efforts with near-surface lapse rates aids in the accuracy and comprehensiveness with which climate change-related issues are explored, and synthesized.

8.2 – Concluding Remarks on Mountain Goat Behavioral Ecology

I investigated the interaction of temperature, mountain goat eco-physiology, and behavior. The use of dual sampling methods allowed for more of a robust sampling design to both mitigate pseudoreplication and facilitate a behavioral ecology study over a relatively short time frame. The complimentary results of scan and focal methods support that scan sampling is an appropriate proxy for time spent on activity, rather than merely a proportion of group behavioral states. Furthermore, applicable results mirrored those of longer-term studies of mountain goats where logistical infrastructure allowed for a collaring program. This study underscores that behavioral ecology investigations for species of interest within at-risk systems can be effectively carried out over short time scales. Given the short study period and the instance of sampling over an unusually cool, high-precipitation summer, I cannot wholly reject that mountain goat activity (in time and proportion) is not affected by temperature. Results nonetheless suggest that mountain goats within the study area mitigate heat stress and thermal variability by shifting

the orientation of budgets though time and space, rather than augmenting or reducing the proportions of behaviors themselves.

Important artifacts of this research are the corresponding results between male and female mountain goats during summer months, both in terms of behavior across periods of day, as well as the analysis on the effect of temperature on goat elevation. Often, ungulate species are rapidly dissected in terms of sex differences because canons of segregation theory lead us to preemptively assume such methods are necessary. This is not to say that sexual segregation has no bearing on mountain goat activity. For example, as was found in many intra-species ungulate studies, female mountain goats spent more time feeding overall, compared to males. This is consistent with the paradigm that increased nutritional and energetic demands are required for gestation, lactation, and individual maintenance during a short growing season. Intersex life histories aside, this research acts as an important reminder that some aspects of an organism's biology are much more fundamental in nature. The risk of susceptibility to thermal stress, need for homeothermic maintenance, need for adequate nutritional gains, and behavioral response to those physiological requirements was common to adult mountain goats. The reason for this is clear: environmental temperature is a fundamental determinant of survival in endotherms. Males and females, despite having varying magnitudes of nutritional need (etc.) both manifested varying behavioral and habitat selection trade-offs by exhibiting the same *type* of change. Males may have relegated a majority of feeding to the morning, whereas females did so primarily in late day. Males may have mitigated heat stress during midday, balancing predation risk by engaging in standing resting behavior. Females may have conserved energy more than males by bedding during midday, strategizing efficiency by synchronizing activities within a large group that decreased the need for time spent in individual vigilance. The overarching theme goes unchanged. Mountain goats decreased activity at midday and made consistent adjustments to their elevation, taking advantage of near-surface lapse rates as a strategy for autonomic thermoregulation, rather than the energetically expensive alternative.

From both an anthropocentric and an ecological perspective, mountain goats are an important indicator species. Seldom does a wildlife species offer such an invaluable opportunity to reveal changes to ecosystem structure, function, and phenology, as well as changes to local climate regimes. Concurrently, this species is a model for the investigation of the most important aspects of mammalian ecology including: population dynamics, sexual segregation theory, optimum forage theory, population and landscape genetics, and physiology. Climate change puts alpine obligates at risk. It remains unclear whether the ecological plasticity demonstrated by mountain goats will allow proliferation of the species, or if they will be extirpated – overtaken by the velocity of climate change. Perhaps southerly populations in the Rockies will fare better, inhabiting a mountain range where 4,000m is a common (almost average) summit elevation. Lapse rates may create thermal refugia in such areas compared to the Coast Range of

Alaska, where 1,500m peaks are already common goat habitat. Perhaps heat dissipation theory and Bergmann's rule will engender the prevalence of behavioral and body-size phenotypes, such that selection for mass and size reductions will allow the species to weather their warming environment. Whatever the case, at a time of rapid environmental change and scant monetary resources invested in biological study, mountain goats are a paragon species for alpine ecology research investment.

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